

WILDFIRE AND MOUNTAIN PINE BEETLE BOUNDARY ZONES: SPATIAL PATTERN, BOUNDARY CREATION AND SUCCESSIONAL CONSEQUENCES

by

ELIOT JONATHAN BENET MCINTIRE

B.Sc. Great Distinction McGill University 1996

M.Sc. Botany University of Toronto 1999

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE STUDIES
Faculty of Forestry

We accept this thesis as conforming
to the required ~~standard~~

THE UNIVERSITY OF BRITISH COLUMBIA
May 2003

© Eliot J.B. McIntire 2003

In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the head of my department or by his or her representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Department of Forest Sciences

The University of British Columbia
Vancouver, Canada

Date June 4, 2003

Abstract

Wildfire and mountain pine beetle (MPB) boundaries are ubiquitous in many forested landscapes, yet they have been rarely described in two-dimensions at the stand-level and their formation and effects on plant community dynamics are poorly understood. Using spatially constrained clustering, the width of seven wildfire and eleven MPB boundaries was determined to be variable and ranged from 0m to 120m (means approximately 30 to 50m). Thus, natural disturbance boundaries varied along a continuum from hard to soft. Using multiple spatially explicit path hypotheses and AIC_c to weigh relative support for each, these boundaries were found to be generated by a combination of stand-level factors as well as unmeasured spatial factors. A key factor was the basal area of susceptible host (for mountain pine beetle) and the basal area of trees that are highly susceptible to fire mortality. The pattern of tree mortality across these boundaries showed little relationship to stand age, stand density, slope or aspect. The spatial trend of mortality across seven of eleven MPB boundaries was sufficiently accounted for by the abundance of susceptible host, indicating that, at these sites, the MPB outbreaks were likely host limited rather than dispersal limited. Using multiple spatially explicit path hypotheses, natural regeneration patterns were found to be primarily driven by a light surrogate across the boundaries. Seed bed and disturbance severity were minor factors affecting the natural regeneration patterns. Seed source and vegetation competition had very little influence on the natural regeneration patterns. Successional trajectories in the boundary zones, as measured by overstory tree abundance and mortality as well as advanced regeneration growth release and natural regeneration patterns, were found to be different than in either the disturbance cores or the intact forest immediately adjacent to the boundary zones. These differences demonstrate that natural disturbances create spatial variation in the boundaries that translates into diverse successional sequences. Forests that have simplified edges, such as the majority of those in a harvested landscape, may have reduced spatial and temporal heterogeneity compared to those with produced by natural disturbance, such as fires and MPB.

Table of Contents

Abstract	ii
Table of Contents	iii
List of Tables	vi
List of Figures	viii
Acknowledgements	xi
Preface	xii
 Chapter 1 General Introduction	 1
1.1 Introduction and context	1
1.2 Objectives and Thesis Outline	3
1.3 Literature Review	4
1.3.1 Ecological Objects and Processes	5
1.3.1.1 Edges and Boundaries	5
1.3.1.2 Natural Disturbance	8
1.3.1.3 Succession	10
1.3.2 Methodology	13
1.3.2.1 Spatial Analysis of Boundaries	13
1.3.2.2 Path Analysis	14
1.3.2.3 Multiple Hypothesis Framework	16
1.3.3 Natural Disturbance and Forest Management	17
1.3.3.1 The Natural Disturbance Paradigm	17
1.4 General Methodology	20
1.4.1 Study Area	21
1.4.2 General Site Selection	21
1.4.3 Data Collection	22
1.4.3.1 General Variables of Interest	23
 Chapter 2 Structural Properties of Natural Disturbance Boundary Zones: Implications for Landscape Heterogeneity	 26
2.1 Introduction	26
2.2 Methods	28

2.2.1	Field Sampling.....	28
2.2.1.1	Study Area	28
2.2.1.2	Sampling Transects	29
2.2.2	Data Analysis.....	30
2.2.2.1	Boundary Delineation	30
2.2.2.2	Boundary Characterization.....	31
2.3	Results.....	36
2.4	Discussion	45

Chapter 3 Understanding Natural Disturbance Boundary Formation Using Spatial Data and Path Analysis 50

3.1	Introduction	50
3.2	Methods	55
3.2.1	Study Area and Study Design.....	55
3.2.2	Transient vs. Non-Transient Factors.....	56
3.2.3	Correlation Analysis	57
3.2.4	Multiple Hypothesis Path Models	57
3.3	Results.....	61
3.3.1	Correlation Analysis	61
3.3.2	Multiple Path Hypotheses.....	61
3.3.3	Influence of Spatial Location.....	62
3.4	Discussion	69
3.4.1	Influence of Spatial Location.....	69
3.4.2	Non-Transient Factors	71
3.4.3	Conclusions	72

Chapter 4 Complex Dynamics of Early Forest Succession At The Boundaries Of Wildfires And Mountain Pine Beetle Outbreaks 74

4.1	Introduction	74
4.2	Methods	77
4.2.1	Field Sampling.....	77
4.2.1.1	Study Area and Study Design	77
4.2.1.2	Advanced Regeneration Growth Release.....	78
4.2.1.3	Field Measurements	78

4.2.2	Vegetation Description and Successional Trajectories	79
4.2.3	Regeneration Hypothesis Testing	81
4.3	Results.....	84
4.3.1	Vegetation Descriptions and Successional Trajectories	84
4.3.2	Natural Regeneration and Understory Growth Release	85
4.4	Discussion	98
4.4.1	Vegetation Descriptions and Successional Trajectories	98
4.4.2	Natural Regeneration and Understory Growth Release	99
4.4.3	Space	100
4.4.4	Implications	101
4.4.4.1	Landscape Modeling	101
4.4.4.2	Long Term Dynamics	101
4.4.4.3	Forest Management	102
4.4.5	Conclusions	102
Chapter 5	General Discussion and Future Directions	104
5.1	Summary of Results.....	104
5.1.1	Revisiting Objectives.....	104
5.2	Conclusions	106
5.3	Is This New?	106
5.4	Implications.....	108
5.4.1	Ecological.....	108
5.4.2	Should Forest Management Create Soft Boundaries?	109
5.5	Why Has This Not Been Studied Before?.....	110
5.6	Future Studies	111
5.6.1	Effect of Natural Disturbance Boundary Zone Variation On Wildlife Habitat Attributes.....	111
5.6.2	Probabilistic Modeling	113
5.6.3	Designed Sustainability: Incorporating Disturbance Boundaries into Management Scenarios	114
	Literature cited	115

List of Tables

Table 1.1 Summary of sampled variables. Techniques for all measurements were taken from BC Ministry of forests field manuals (Armleder et al. 1992; Meidinger et al. 1998).....	25
Table 2.1. Summary and properties of sampled sites.....	35
Table 3.1. Correlation matrix of Pearson correlations between all independent variables and BA dead (dependent variable throughout) for all sites sampled.....	65
Table 3.2. Path model results. Numbers represent AIC _c differences (Δ_i). Bold= $\Delta_i < 3.84$, underline=CFI>0.95, *=RMSEA<0.06. # times best model is where $\Delta_i = 0.0$. # times <3.84 is where the path model is statistically indistinguishable ($P(\chi^2 3.84=0.05)$). # good models is where both Δ_i and either RMSEA or CFI were considered the path model good.	66
Table 3.3. Akaike weights, $w_i = \frac{\exp(-\Delta_i / 2)}{\sum_{r=1}^R \exp(-\Delta_r / 2)}$. These can be interpreted approximately as the probability that a model is the best model (Burnham & Anderson 2001). Weights >0.05 are indicated by bold typeface.	67
Table 3.4. Proportion of sites for which each relationship has a significant path coefficient ($p < 0.05$). This is equivalent to a significant regression coefficient in a multiple regression. Sites with significant values for density (F11, M14) and age (M2, F18) did not have support for the path models 2 and 5, respectively.....	68
Table 4.1. Summarized results of statistical tests used to characterize the state of the overstory and understory trees and vegetation for all sites. Test significance levels are set to $p=0.01$. “N” and “Y” indicate non-significance or significance, respectively. “IF”, “BZ”, and “DC” indicate intact forest, boundary zone and disturbance core, respectively. See text for details for each statistical comparison.	88
Table 4.2. Successional trajectories following natural disturbances in the remaining intact forest, the boundary zone, and the disturbance core. Noted is when the boundary zone is different from both the intact forest and the disturbance core. These results are based on the dichotomous key in Figure 4.2. Sites F18 and F19 had no detectable boundary zone.	91
Table 4.3. Path model results for shade tolerant regeneration species. Numbers represent AIC _c differences (Δ_i). Bold= $\Delta_i < 3.84$, underline=CFI>0.95, *=RMSEA<0.06. # times best model is where $\Delta_i = 0.0$. # times <3.84 is where the path model is statistically indistinguishable	

($P(\chi^2 3.84=0.05)$). # good models is where both Δ_i and either RMSEA or CFI were considered the path model good. K=number of parameters in the model.	92
Table 4.4. Path model results for shade intolerant species. See Table 4.3 for details.	93
Table 4.5. Path model results for understory growth release. See Table 4.3 for details.	94
Table 4.6. Akaike weights, $w_i = \frac{\exp(-\Delta_i / 2)}{\sum_{r=1}^R \exp(-\Delta_r / 2)}$. These can be interpreted approximately as the probability that model is the best model (Burnham & Anderson 2001). Weights >0.05 are indicated by bold typeface.	95
Table 4.7. Significant standardized coefficients (r) based on multimodel averaging, weighted by the relative (AIC_c) strength of the model. “—” indicates not sufficient regeneration counts to perform analysis. Veg. indicates competition from understory vegetation. Bold: $p<0.01$; Not bold: $p<0.05$	96
Table 4.8. Proportion (and number) of sites that each relationship has a significant path coefficient on natural regeneration ($p<0.05$) within a model that is selected as being the “best” models (based on AIC). This is equivalent to a significant regression coefficient in a multiple regression, but only from those models that are considered absolutely ($CFI>0.95$ or $RMSEA<0.06$) and relatively ($\Delta_i<3.8$) good.	97

List of Figures

- Figure 1.1. Design of sampling transect with an example of a soft boundary delineated by inner and outer boundaries showing the intact forest zone, boundary zone and disturbance core zones..... 24
- Figure 2.1. Methodology for identifying minimum and maximum severity spatial clusters and for calculating minimum boundary zone (MinBZ) and maximum boundary zone (MaxBZ) width. For clarity, only the distances from low severity plots to the nearest high severity plots are shown. A similar number of linear measures were identified from each high severity plot to the nearest low severity plot. Cluster colour ranges from white (0% mortality) to black (100% mortality). Symbol colour: White=peak severity clusters; black=minimum severity clusters; diamonds=minimum distance estimate; crosses=maximum distance estimate (where applicable). A. Maximum width estimate. B. Minimum width estimate. 33
- Figure 2.2. Sinuosity calculation for site M13, 5m plot. Sinuosity is calculated as actual boundary length divided by minimum boundary length for each inner and outer boundary. Lines would link closest plots; diagonals were therefore not used unless there were missing data and a diagonal move was the closest. Symbols: circles = 5m plot centers. Lines: solid = shortest possible boundary given the shape of the transect; solid = actual measured boundary; white: inner boundary; gray = maximum outer boundary; black = maximum outer boundary. Cluster colour ranges from white (0% mortality) to black (100% mortality)..... 34
- Figure 2.3. Peak severity of disturbance event based on the maximum severity clusters (BA killed/[BA killed + BA alive]). Black=Fires; Grey=MPB. Error bars indicate 95% confidence limits (see Table 2.1 for sample sizes). 38
- Figure 2.4. Sample goodness-of-fit graph. Site F12, 5m resolution, corresponding to Figure 2.5A. In this sample, 22 clusters were selected. Alternatively, 11 clusters could have been selected, but mostly single plot clusters were created..... 39
- Figure 2.5. Cluster maps of four sites with points used for calculating distances. Cluster colour ranges from white (0% mortality) to black (100% mortality). Symbol colour: White=peak severity clusters; black=minimum severity clusters; diamonds=minimum distance estimate; crosses=maximum distance estimate (where applicable). Inner boundaries are represented as

the line connecting black symbols; outer boundaries are the line connecting white symbols.	
A) Site F12, 5m plots; B) Site F20, 10m plots; C) Site M13, 5m plots; D) Site M16, 20m plots.....	40
Figure 2.6. Histogram of boundary widths by plot size, disturbance type, and estimation type.	
Means are indicated on each graph. Black=Fires; Grey=MPB. Wilcoxon rank sum tests, *: $p < 0.05$	41
Figure 2.7. Steepness of boundaries. Black=Fires; Grey=MPB (units are % severity change per meter $\pm$ 95% C.I.). Wilcoxon rank sum tests, *: $p < 0.05$	42
Figure 2.8. Sinuosity of boundaries. Black=Fires; Grey=MPB (units are inner boundary length/straight length + outer boundary length/straight length $\pm$ S.E.). Wilcoxon rank sum tests between fire and MPB, n.s.: $p > 0.25$	43
Figure 2.9. Between plot variance in severity within each of three zones: inside the disturbance, in the boundary zone (B.Z.) and outside the disturbance. See text for MaxBZ and MinBZ. Probability levels are shown comparing the three zones for fire and MPB (Kruskal-Wallis (SAS Institute Inc. 2000)).	44
Figure 2.10. Proportion of the total disturbance area in a hypothetical circular disturbance that is contained within a 50m wide boundary. Calculations were made based on 50% of the boundary zone being included within the stated disturbance size.	49
Figure 3.1. Hypothesized path models. All error terms are left out of the diagrams for clarity. Every endogenous (has a hypothesized factor affecting it) variable has an error term representing all unmeasured factors that influence the variable. Since there is only one exogenous factor (space), there are no unresolved covariances.	54
Figure 3.2. Histograms of standardized correlation coefficients of the a) effect of space on susceptible trees and b) influence of basal area of susceptible trees on mortality. X-axis represents the middle of the histogram bin ranges. Black=fire, gray=MPB.....	63
Figure 3.3. Histograms of standardized correlation coefficients of the influence of space on mortality. a) total, b) direct and c) indirect effects of space are shown. X-axis represents the middle of the histogram bin ranges. Black=fire, gray=MPB.....	64
Figure 4.1. Path models. Note for analyses on advanced regeneration growth release (Release) the variable Seed Source is replaced throughout with Severity and LFH depth is removed.	76

Figure 4.2. Flow chart of successional descriptions used in this paper. Release indicates advanced regeneration growth release (see text). Questions 1, 2, 3, 4 and 9 do not require comparison with the intact forest as a control. Demarcation for questions was $p < 0.01$. See Table 4.1 for complete results. 87

Acknowledgements

I owe many thanks to several people and organizations that helped during the course of this thesis. I was funded by an NSERC PGS-B graduate scholarship, a University of British Columbia UGF scholarship, a Donald S. McPhee Fellowship from the Faculty of Forestry, a research assistantship from a collaborative NSERC research grant with International Forest Products and several TAs through the Faculty of Forestry. I am grateful to Arrow Lakes Innovative Forest Practices Agreement from 2000-2002, and in particular to Paul Jeakins and Kokanee Forest Consulting, Nelson, BC for the research money without which this thesis could not have been done. I thank the Faculty of Forestry and Department of Forest Sciences, UBC for logistical support throughout.

I would like to thank my committee members for direction and support at each step along the way. I thank Stephen Mitchell for pushing me from the start to the finish and alerting me to the flaws of overconfidence. To David Andison, I am grateful for the extremely valuable landscape perspective that will likely be the direction of much of my future research. I thank Marie-Josée Fortin for her timely arrival in Vancouver within months of my own and for giving rigour and structure to my mental research maps that had been with me for many years, but had been unable to express themselves. I would like to thank Hamish Kimmins for inspiration from before I started this PhD until now and likely beyond. He also gave me the opportunities to pursue my ideas by getting my foot in the door when money was at stake. Finally, while there may still be a part of him that wished I had worked on western larch, a topic he had brought up many times in the early phases, I felt honoured as the conversations over the years grew to have a profound reciprocal respect for each other's ideas. I thank John Nelson, Gary Bradfield, and William Fagan (University of Maryland) for taking the time to read my dissertation as External Examiners at my oral defense and for imparting their wisdom on me and my dissertation.

During my stay at UBC, I also had help and inspiration from numerous people. I would like to thank Brad Seely for teaching me FORECAST, being instrumental in getting me financial support in the last year, and providing great feedback throughout. To David Tait, I am grateful for the persistent orthogonal thinking and the guidance to be an ecological detective. I would like to thank David Huggard for teaching one of the most moving courses—Research Methods—I have ever taken, though I didn't realize it at the time. I would like to thank Ben Gilbert, Ben Andrew, Corey Bird, and Judy Rodriguez for the long hours of field work and the grueling climbs in the West Kootenay Mountains. This thesis could not have been done without you. This thesis was greatly improved by conversations with several graduate students and researchers: Adrian Weber (who sadly passed away within months of my arrival), Clive Welham, Rob Serrouya, Geraldine Jordan as well as many others. To Robin Duchesneau, to say that this thesis was improved by conversations with you would be a gross understatement: the never ending questioning, challenging, humour, coffees, and shared beers made my time at UBC truly outstanding and pushed me to places that I never would have thought I could go. Thank you Robin.

I would like to thank Catherine Rigg, Charlotte Gjerløv (det var en sand fornøjelse), Derek Ray, and Sonia Talwar for the profound friendships and support throughout these four years. À Céline Boisvenue, merci pour être venue dans ma vie et pour l'aide sur la thèse, l'inspiration, l'amitié, et l'amour que tu m'as donnés. Finally, I thank all the members of my family—Olivia, Matthias, Rebekah, Harley, Gabrielle, my father, Thomas, and my mother, Carolyn—for unending support and love that have brought me to where I am.

Preface

This dissertation has been written in the “chapter-as-manuscript” format. Chapters 2 through 4 are data chapters presented in publication style format with independent introductions, methods, results, and discussions. Chapters 1 and 5 are the bookends enclosing these three data chapters. Chapter 1 provides a broad introduction that includes a literature review of the topics important to the dissertation, overall objectives and general field methods. Chapter 5 provides a general discussion of the dissertation that includes a summary and contextualization of results, general conclusions, and directions for future work. Chapters 2 to 4 contain sufficient information to be standalone research pieces and contain some redundancy. In particular, the methods sections have some overlap in the field site descriptions, but each is slightly different and focuses on the particular aspects of the field sites that are essential for understanding the chapter. Furthermore, the introductions to each chapter have some redundancy with the general literature review in Chapter 1. Since each chapter focuses on a specific component of the general topic of boundaries, there are unique features included in the introductions of each data chapter. Each data chapter has a discussion that is meant to interpret and conclude the results in the context of that chapter. The final chapter (Chapter 5) is a general discussion and ties the results and interpretations from each data chapter into the single framework of a PhD thesis.

Chapter 1 General Introduction

1.1 *Introduction and context*

Landscape forest boundaries, particularly those from wildfires and mountain pine beetle outbreaks, are ecological phenomena that influence species colonizations (Chen et al. 1992; Greene et al. 1999), species invasions (Cadenasso & Pickett 2001), species interactions (Fagan et al. 1999), biodiversity (Leopold 1933), predator and prey movement (Forman 1995), bird nest predation (Saracco & Collazo 1999) and play numerous other roles (Herlin 2001; Schonewald 2001). Much of this research on forest boundaries, however, has been based primarily on hard edges¹, and has been called the “edge effect” (Leopold 1933; Kremsater & Bunnell 1999; Cadenasso & Pickett 2001; Honnay et al. 2002; Huggard & Vyse 2002). Information gained about the edge effect from hard edges may be a special case of forest boundaries that are generally more spatially complex (Leung 1987) and about whose function and effects we know very little. Unfortunately, it is difficult to determine whether edge effect research is indeed a special case because the spatial extent and complexity of naturally produced forest boundaries as two dimensional phenomena has attracted little attention (though see Kent et al. 1997; Fortin et al. 2000). Furthermore, the different functions of soft and hard boundaries have been poorly addressed and for only a limited set of ecological phenomena, such as bird nest parasitism (Ratti & Reese 1988; Saracco & Collazo 1999). The description and understanding of natural disturbance boundaries as well as their implications for other ecological phenomena, such as natural regeneration, are poorly known.

In addition to the numerous influences of natural disturbance (ND) boundaries on ecological processes and patterns, these boundaries may also provide information for ecosystem based forest management (Attiwill 1994b) and, in particular, the emulating natural forest disturbance paradigm (ENFD) (Bergeron & Harvey 1997; Perera et al. 2003). Within ENFD, NDs have been identified by many as a useful coarse-scale ecological process to guide forest

¹ Two classes of terms have been used in ecology and forest management in the study of edge diffuseness. In this thesis, the term “soft” will be used to indicate edges that can have been described as “fuzzy”, “complex”, “low contrast” and “gradients”. To indicate edges that are “abrupt”, “high contrast” and “sharp”, I will use the term “hard”. Chapter 2 in this study provides a functional and quantitative definition of edge diffuseness.

management (Galindo-Leal & Bunnell 1995; Parsons et al. 1999; Swetnam et al. 1999; Spence & Volney 1999). Indeed, ENFD has been ubiquitous in forest management literature for at least ten years (Hunter 1993; Attiwill 1994a; Attiwill 1994b; Christensen et al. 1996; Bergeron & Harvey 1997; Adamowicz & Veeman 1998; Landres et al. 1999; Parsons et al. 2000) and has formed one of the bases for sustainable forest practices in British Columbia for eight years (Ministry of Forests & Ministry of Environment 1995). The ENFD paradigm refers primarily to a seral stage frequency characteristic for a given landscape based on the historical fire regime, though it is not limited to this (e.g., remnant patch abundance and placement (Andison & Cumming 2001)). Some implementations of the ENFD paradigm are inappropriate and limited because some natural disturbances are too large such that emulating them is not socially acceptable (e.g., large campaign fires in Canadian Boreal forest). In general, management implementation of this coarse-scale approach has been patch-centric, not allowing for between-patch variation. New and innovative ecological insights about natural disturbance processes, such as descriptions and understanding of boundary complexity, should be developed and imported into policy. The creation of spatial variability at the boundaries of harvested patches would be a relatively easy characteristic of NDs to implement.

One possible reason for the dearth of stand-level empirical descriptions of natural disturbance boundaries is the difficulty in describing two-dimensional boundaries in a simple, intuitive, and practical way. This process of delineating boundaries in a complex world has a long history (Schonewald 2001). For instance, classification techniques have been used for subjectively delineating boundaries (e.g., between species) for centuries (Darwin 1860). But, as soon as species boundaries were drawn, it was apparent that intermediates ("hybrids") existed and that they often played disproportionately important roles (e.g., Barton & Hewitt 1985; McIntire & Waterway 2002). Historically within ecology, boundary analysis began by identifying the presence of boundaries and by examining the effects of simple boundaries on neighbouring ecosystems (e.g., the edge effect). Quantitative techniques have been developed and used to objectively determine where boundaries exist in complex systems (Fortin 1994; Jacquez et al. 2000). In some instances, however, the boundaries themselves may be spatially complex and this complexity may contribute to unique ecosystem properties (Ratti & Reese 1988). Several techniques have been used to quantify soft boundaries, including fuzzy modeling (Leung 1987; Jacquez et al. 2000) and fractal analysis (McQuillan 2000). These techniques may

not be appropriate for stand-level understanding and descriptions of natural disturbance boundaries because of the data requirements for the former and difficulty to interpret fractal geometry. To date, adequate stand-level techniques for describing natural disturbance boundary complexity are not readily available.

There are two broad contexts and reasons to undertake this study. First, ND boundaries are poorly described and poorly understood, and the influence of ND boundaries on forest structure and function is unknown. Informal suggestions indicate that boundaries in NDs are not always hard and that a large level of local heterogeneity exists along natural boundaries, but there is little empirical stand-level data to support this. This thesis will describe, analytically model, and examine the consequences of wildfire and MPB boundaries, thereby beginning to fill this knowledge and data gap. Second, this thesis addresses a question within the ENFD paradigm and seeks to provide suggestions for forest management within this context. Furthermore, the ENFD paradigm has generally focused on fires, which are not the only natural disturbances in many regions. This study will examine mountain pine beetle and wildfire boundaries to quantify and compare their attributes for a broader basis on which to base forest management recommendations.

1.2 Objectives and Thesis Outline

There are three broad objectives in this study, each of which is addressed in a chapter of the thesis. These objectives and several research questions within each are:

Chapter 2: to examine, delineate, describe and compare the spatial patterns of the boundaries created by fires and mountain pine beetle.

- a. Can spatially complex boundaries be defined and delineated at the forest stand scale?
Can spatially constrained clustering be used to objectively describe complex boundaries?
- b. Do NDs create soft boundaries? In other words, do they create two-dimensional areas of land rather than linear entities (this will be a question of scale)? What are the width, steepness, sinuosity, and heterogeneity of the boundary zone? Are these values a function of the plot size used (5m, 10m, and 20m)? Is the boundary zone more heterogeneous than the intact forest or disturbance core?
- c. Do MPB and fires differ in their spatial patterns at the boundary?

Chapter 3: to quantify stand-level factors that affect the mortality pattern across the boundary.

- a. Boundary creation is a multi-factorial, multi-scale process related to properties of a disturbance. What are the relative influences of aspect, slope, tree species, tree age, and tree density at the stand-level and how do they contribute to the cessation of the disturbances?
- b. Can a path analytical framework be used to separate direct and indirect influence of spatial configuration of tree mortality across the boundary?

Chapter 4: to examine the influences of NDs on early post-disturbance successional dynamics within boundary zones (Chapter 4).

- a. Are the successional pathways initiated within a boundary different from those adjacent to the boundary zone? Are these successional pathways intermediate between the disturbance opening and the intact forest, or are there non-linear responses to overstory mortality?
- b. Are release of advanced regeneration and seedling abundance related to local characteristics including disturbance severity, light, understory vegetation, and seed source?

Broadly speaking, these chapters address spatial pattern of the boundary (Chapter 2), the factors influencing the creation of the boundary (Chapter 3), and early post-disturbance succession at the boundary (Chapter 4). I purposely frame these dissertation goals as objectives here and present detailed graphical hypotheses (path models) in Chapters 3 and 4. Chapter 2 is descriptive and Chapters 3 and 4 test multiple hypotheses and are therefore deductive.

1.3 Literature Review

This review highlights several papers in each of the topics listed below and guides the reader to current knowledge gaps, omissions, and important future considerations. Furthermore, in some of the topics, substantial criticism of the current approaches is presented within a framework of possible solutions. The review will proceed using the following structure:

- Ecological objects and processes
 - Edges and boundaries
 - Natural disturbances
 - Forest succession
- Methodology

- Spatial analysis of boundaries
- Path analysis
- Multiple hypothesis framework
- Conceptual foundation for forest management
 - Current forest management

This structure introduces three large topics of ecological importance in this thesis. Edges and boundaries form the overall framework for the questions that are addressed. Natural disturbances are the primary processes that create the boundaries being studied; understanding the disturbances is essential for understanding the formation of the boundaries. Forest succession is the phrase used in this thesis to describe the temporal patterns of overstory and understory development and is the key topic in Chapter 4. Since this thesis has a strong methodological component, reviews of three key methodologies used here are presented. Finally, the overall context for this study is that natural disturbances are being proposed by proponents of EFND as coarse filter templates for management to emulate.

In general, there is a lack of ecological literature related to complex boundaries. Thus, in many sections, e.g., forest succession, there is little focus on the “literature of succession at boundaries”, largely because there is little literature that explicitly examines these topics. Instead, these reviews take a more general approach.

1.3.1 Ecological Objects and Processes

1.3.1.1 Edges and Boundaries

1.3.1.1.1 The Edge Effect

The influence of forest edges on openings and forest interior —dubbed “the edge effect”—has long been known (Leopold 1933). The edge effect has mostly been studied in tropical forests and for animal and bird effects (Murcia 1995) with less focus on temperate (Cadenasso et al. 1997) and conifer forests (Wiens et al. 1985; Chen et al. 1992).

Edge effects have been variously defined, but the primary notion is the horizontal influences that occur between neighbouring ecological communities. In the context of forests and forest management, the edge effect is usually the effect of a harvest opening into the intact forest or the effect of the intact forest into the harvest opening. The edge effect in this context is

a linear measure (e.g., depth in meters) into or outwards from the edge. Quantification (Rusek 1992; Cadenasso et al. 1997; Harper & Macdonald 2001) of the edge effect has been made for at least 50 years (Reifsnyder 1955; Geiger 1965). The edge effect may be different for each variable and is often measured separately for each (Huggard & Vyse 2002). Some variables that have been measured and show an edge effect include microclimatic variables such as light, temperature and wind (Chen et al. 1992), microenvironmental variables, such as moisture and nutrients (Matlack 1993a), and plant variables, such as community and population dynamics (Palik & Murphy 1990; Meiners & Pickett 1999), invasive species (Honnay et al. 2002) and natural regeneration (Greene & Johnson 1996). Bird ecologists have shown great interest in edges because nest predation appears to increase dramatically (Gates & Gysel 1978; Yahner 1988; Hartley & Hunter 1998; McCollin 1998; Luck et al. 1999; De Santo & Willson 2001). In general, the depth of edge effect varies from <5m to 100's of meters depending on the organisms or variable of interest and the height of the trees (Lehmkuhl & Ruggiero 1991; Forman 1995; Kremsater & Bunnell 1999).

One aspect of the edge effect literature is the often subjective attribution of positive or negative to the overall effects. This is invariably linked to a cultural or research driven value-based qualification. For instance, when Aldo Leopold first described the edge effect, he was referring to the positive effect of edges on game species (1933). In a review of the effect of edges in fragments, Murcia (1995) examined research studies for their positive or negative influence on abiotic and biotic characteristics. At the time of her review, the term "edge effect" was presumed to be deleterious (Murcia 1995). This sentiment was driven by the conservation ethic that valued preservation of species that required interior forest conditions (i.e., without influence of edge). The realization that the edge effect reduces the overall area of intact forest in disturbed areas has raised the issue of edges as a major concern in conservation. If there is a general pattern, there appear to be some organisms whose numbers are increased, some whose numbers are decreased, and others that appear largely unaffected by edges (Murcia 1995).

The influence of edges on abiotic factors is relatively easy to determine, but the spatial extent of this influence varies between different forest types. Studies have demonstrated that in tall forests, changes in wind speed can be detected into the intact forest to between 40m and 240m from the edge (Raynor 1971; Chen et al. 1992). Temperature has been modeled across boundaries and appears to be influenced up to 40m into the forest (Saunders et al. 1999).

Changes in light generally appear to be altered over a shorter distance than wind or relative humidity (Matlack 1993a; Gehlhausen et al. 2000). Plant species, including trees, will likely respond to the character of these microclimatic gradients.

The influence of edges on natural regeneration has been studied extensively, but no simple relationships have emerged yet that allow for good prediction (Greene et al. 1999; Duchesneau, *pers. comm.*). Currently, there are few studies on general patterns of regeneration at forest edges. In general, much of the work to date has focused on species-specific dispersal functions that describe the distance traveled by seeds (usually into an opening). Several authors have attempted mechanistic, deterministic descriptions of this (Greene & Johnson 1989; Greene & Johnson 1994; Greene & Johnson 1996; Greene et al. 1999). Some alternate work underway attempts to spatially model regeneration distribution in openings based on a selection of possible seed dispersal statistical distributions which do not rely so heavily on deterministic assumptions (Duchesneau 2003). Clearly, where there is such process uncertainty, deterministic models have reduced value because it is the extreme events (e.g., seed masting) that not only affect the outcome but may be the primary cause of the observed pattern. For example, Greene et al. (1999) found that deterministic functions can be off by three-fold in their predictions of seed densities.

1.3.1.1.2 The Boundary Zone

The concept of the edge effect has some weaknesses since the edge effect is only a subset of the possible influences of forest boundaries. In locations where the boundary between two communities is not a hard edge, a more general concept of boundary zone is necessary. The ecological importance of zones with “intermediate characteristics” between neighbouring homogeneous stands is largely unexplored with only a few explicit studies addressing boundary ecology and boundary dynamics (Wiens et al. 1985; Ratti & Reese 1988; Holland et al. 1991). The studies that have been done on the effects of different types of boundaries in harvested landscapes suggest that there are significant differences in ecological features between hard and soft edges (Ratti & Reese 1988; Suarez et al. 1997; Cadenasso & Pickett 2000). For example, at least one study showed virtually no nest predation at what they describe as gradual (soft) edges as compared to the high nest predation at the hard edges (Saracco & Collazo 1999). Overall, however, there is very little research on the ecology of the boundary zone.

1.3.1.2 Natural Disturbance

There are many reviews of fires and other natural disturbances, their ecology, interactions between disturbance agents, and the relevance for management (Pickett & White 1985; Crane & Fischer 1986; Whelan 1995; Rogers 1996; McCullough et al. 1998; Parminter 1998; Edmonds et al. 2000; Brown & Smith 2001; Frelich 2002).

1.3.1.2.1 Fires and Edges

Fires are one of the key processes that influences regions, landscapes, stands, and individual plants in many ecosystems (Pyne 1995; Crawley 1997a). There are several general fire ecology introductions that discuss fires and fire ecology in North America (Whelan 1995; Kimmins 1997; DeBano et al. 1998). More regionally specific works have also been published that describe fires and their effects in southern British Columbia (Crane & Fischer 1986; Agee 1993). Specific works on the interactions between plants and fire demonstrate the complexity and reciprocal nature of these interactions (Bond & Wilgen 1996; Brown & Smith 2001). There are also several introductions to fire in the context of forest management (Rogers 1996; Schmoltdt et al. 1999). Fires have been extensively classified for purposes of fire suppression, fire management, and fire regime (Brown & Smith 2001). However, in spite of the diversity of fires and their effects, fires are often classified as either stand replacing or stand maintaining (Ministry of Forests & Ministry of Environment 1995). While the conflict between this fire regime simplification and maintaining complexity is recognized (Brown & Smith 2001), the implementation of fire management strategies has usually been based on the simplification (Ministry of Forests & Ministry of Environment 1995). Where complexity and heterogeneity are important for some ecological processes, such as may be the case in forests and wildfires, simplification of fire regimes may lead to management decisions that lead to simplified landscapes.

Components of the forest can alter the spread of fire. For instance, changes in tree species composition as a fire progresses across the landscape can cause a reduction in fuel loads and burning intensity and act as a natural fire break (Cumming 2001b). Tree density can be manipulated to reduce fire propagation (Graham et al. 1999); though it is unclear how much effect naturally occurring variation in tree density has on fire characteristics and behaviour. Forest models, such as BEHAVE, explicitly model a large set of mechanistic processes,

including surface fire spread, intensity, flame length, area and perimeter of a point source fire, spotting distance, probability of ignition, scorch height, tree mortality, containment, with options to simulate containment, suppression, transition to crown fire, crown fire spread, fuel burnout behind the fire front, emission production and soil heating (Andrews & Bevins 2002). There has been very little modeling of the cessation of a fire. Of the trio, fire ignition, propagation and cessation, the latter is the least understood. An analysis of ND boundaries and the causes of boundary formation can lead to understanding and model parameterization for this disturbance cessation.

The characterization of fire regimes is of great importance for the study of fire disturbance boundaries. Some authors have defined fire regimes based primarily on fire severity (e.g., Agee 1993). Others have included fire frequency and fire size (Cissel et al. 1998). In spite of an explicit awareness of the spatial variability in fire severity (Agee 1993), there are few quantitative analyses of what contributes to the spatial pattern of fire. Even in forest dominated by stand replacing disturbance regimes (e.g., Western Canadian Boreal forest), there is substantial variation in fire severity (e.g., Andison 2001). Clearly, in addition to the usual factors used to describe a fire (e.g., severity, frequency, size, etc., see White & Pickett 1985), spatial variability and where that variability occurs are two of the features that are lacking in our understanding of fire ecology.

1.3.1.2.2 Mountain Pine Beetle and Edges

The mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopk. (Col.: Scolytidae), is a bark beetle that kills trees following a successful attack (Safranyik et al. 1999). It is a dominant ND agent in western North America (Samman & Logan 2000). Total mortality in a MPB outbreak can be immense, totaling hundreds of thousands of hectares per year in BC. These numbers, however, can be somewhat misleading because, in many cases, it is likely that not all trees in the stand are killed. Indeed, the classification scheme used the Ministry of Forests to indicate outbreak severity considers the highest category of mortality to be >30%. Overall, MPB plays a critical role in development, senescence and reestablishment of many western forests (Redfearn & Pimm 1987; Samman & Logan 2000).

While MPB disturbances are different in many characteristics from those of fires, some traits may be similar. Indeed, it is often shown that, unlike a fire, an insect outbreak causes a

shift in tree species to shade tolerants (Kneeshaw & Bergeron 1996; Edmonds et al. 2000). This may not always be true. The impact of a MPB outbreak on stand development or succession is a function of the severity of the outbreak and the understory vegetation. Some studies of episodic outbreaks of major defoliators have shown an effect that is similar to that of surface fires in directing succession (Holling 1981). If there is 100% mortality of trees in a stand that has little understory vegetation and semi-serotinous cones, these can be heated sufficiently to release seeds and allow for seedling regeneration. Such a MPB outbreak would be stand replacing. In cases where there is an intact understory of shade tolerant tree species (such as subalpine fir), the overstory mortality will cause a release of this understory tree regeneration and likely lead to a shade tolerant stand. In a study at Lac Duparquet, Quebec, the effect of spruce budworm (*Choristoneura fumiferana*) in older conifer stands was to revert them to an earlier seral mixed conifer/deciduous stand (Bergeron & Dansereau 1993). In spatially variable MPB outbreaks or fires, successional trajectories may be stand replacing, stand maintaining, stand accelerating and stand altering.

1.3.1.3 Succession²

Like fires, there is a large literature on forest succession. Throughout the past century there have been some longstanding debates beginning with two opposing ideas that succession is driven by individualistic processes or is driven by whole communities (Clements 1916; Gleason 1926). There are a handful of “classic” papers that have created and modified our theories of forest succession. Throughout these papers, several theories and terms have been created or used to describe successional trajectories³. These include facilitation, inhibition, and tolerance (Connell & Slatyer 1977); initial floristics and relay floristics (Egler 1954); monoclimate and polyclimate (Tansley 1920); multipathway (Fastie 1995); equilibrium and non-equilibrium

² This mini-review and critique of succession departs substantially from a standard review. I first demonstrate the rich history of the succession literature, but do not delve into the papers. Instead, I critique the field while resituating the components in a different context. I then conclude with a call for increased complexity (including spatial complexity) for a richer functional understanding of forest succession.

³ A temporal snapshot of the combined overstory and understory plant species composition as it relates to the potential for community change over time. This refers particularly to understory regeneration, advanced regeneration growth release and mortality in the overstory due to disturbances, but also includes herbs and shrubs.

(Turner et al. 1993); individualistic and superorganism (Gleason 1926); climatic climax and edaphic climax; resource ratios (Tilman 1985; Tilman 1987); allogenic, autogenic and biogenic; life history traits (Odum 1969; Drury & Nisbet 1973; Cattelino et al. 1979); primary and secondary succession (Cooper 1923a; Cooper 1923b); hierarchies of successional causes (Pickett et al. 1987a); succession models (Shugart & West 1980; Huston & Smith 1987; Smith & Huston 1989). Many literature reviews have included discussions of these papers (Horn 1974); (Thoreau 1860; Tansley 1920; Cooper 1923a; Cooper 1923b; Gleason 1926; Egler 1951; Whittaker 1953; Egler 1954; Odum 1969; Drury & Nisbet 1973; Shugart & West 1980; Noble & Slatyer 1981; Pickett & White 1985; Tilman 1985; Huston & Smith 1987; Tilman 1987; Halpern 1988; Smith & Huston 1989; Fastie 1995; Crawley 1997b).

None of the theories presented in this mini-review is a true theory; none of the "theories" can be falsified (Popper 1979; Peters 1991). The "theory of the monoclimate community" is not falsifiable because every time it is falsified, the advocates state that an exception has been found. Thus, a better way to conceive of these "theories" is by thinking of them as "modes of thought". Every mode of thought provides a contribution and may be applicable in a specific set of circumstances or study goals. The mode of thought of the hierarchy of successional causes (Pickett et al. 1987b), for instance, allows us to consider many species-level mechanisms of succession. It gives us no predictability in a given location; we have no understanding of why a given factor is important in a given situation and not in another; we have no explanation for emergent properties, such as community diversity and stability. The hierarchy of successional causes also gives no notion of how often nor how important a given factor is in a given landscape in comparison to other factors.

Although no single mode of thought has found true general applicability, ecologists discuss, debate, predict and understand successional trajectories. We use terms that have a *functional* understanding such as "early seral species" and "climax". Most ecologists can identify an early seral species (e.g., *Populus tremuloides* Michx., *Epilobium angustifolium* L.) and can use the term with broad understanding. Confusion arises when these functional understandings break down for the exceptions. Western redcedar (*Thuja plicata*) has many features of both early seral species and late seral climax species (Burns & Honkala 1990). These exceptions form much of the debate about successional theories: a general theory should be able to account for the exceptions.

The quantity of papers related to the creation of a “general theory of succession of plants” is difficult to fully encompass in a single review. This indicates that either, 1) there is no generalized theory of succession yet created, 2) there can be no *generalizable* theory of succession because it is ultimately multifactorial in time, space and scale, or 3) there are many suitable general theories, each with sufficient predictive and descriptive power, and each appropriate depending on the particular perspective of the reader. This last option indicates, perhaps, that there are only specific theories of plant succession and the quest continues to find the general theory (Margalef 1963). Where does this leave succession ecologists? Are there any new ideas that are changing the way we perceive succession?

A generalized theory will, likely, not come from an individual, a population, a community, an ecosystem or a landscape perspective. Each level of organization has real processes, real context, and real questions that need to be answered. However, there are too many processes or mechanisms that all function simultaneously. Instead, a general theory will likely come from a systems analysis or a thermodynamic perspective. In each of these, a large set of interacting variables is subsumed under more comprehensive but fewer variables that have general reality. Following from the successes of physics, thermodynamics-based ecology uses joules, entropy, exergy and other “fundamental” variables that cross many scales (Jørgensen et al. 1992; Jørgensen 1992; Muller et al. 1992; Ulanowicz 1997; Kay 2000). The problem with these perspectives, however, is that they subsume many interesting features of the biological world—such as species, communities—into simple quantities that are very abstract, such as entropy (Kay et al. 2001). In many systems, however, a utilitarian view of the ideas of the late Rob Henry Peters (1991) concerning prediction of ecosystem dynamics may be the most useful in many situations. This may require knowledge of spatial and temporal complexity.

Numerous new works incorporate ecosystem complexity into theories of succession. For instance, disturbance, scale and spatial complexity have been best addressed by Lee Frelich and coauthors. Few other authors have demonstrated the presence of non-linear dynamics, threshold responses, and simultaneous successional dynamics within the same disturbance (Frelich & Reich 1999; Frelich 2002). Other works have taken explicitly non-equilibrium dynamic ideas and applied them to plant community change over time (Chesson & Case 1986; Sprugel 1991; Turner et al. 1993; Cumming et al. 1996). In many cases, these works depart significantly from most of the other theories of succession. Not only are plant communities not predictable, the

forces that are directing them are changing as fast or faster than the time it takes to reach any sort of climax. Thus, no steady state would occur in a landscape because of changing climate, changing effects of seed dispersal based on the previous disturbance state, and changing local species compositions. Even in simple three species “communities”, the temporal dominance may be inherently unpredictable (Huisman & Weissing 2001). This fundamental chaotic nature of succession can be seen in other “non-chaos” studies that have demonstrated that seed source and initial conditions determine the outcome of succession (e.g., Abrams et al. 1985). These papers on the influence of various types of complexity—spatial, temporal, scale—on forest succession represent one of the new directions of succession research.

1.3.2 Methodology

1.3.2.1 Spatial Analysis of Boundaries

Boundary delineation—the process of determining where a boundary is and the characterization of its structure—ranges from a simple visual estimation of changes in some ecosystem variable across a transition (Lloyd et al. 2000) to more sophisticated mathematical procedures to objectively draw lines on the landscape (Oden et al. 1993; Fortin 1994; Fortin & Drapeau 1995). In places where the edge is deemed to be hard, studies usually choose the exact location of the edge subjectively (e.g., Harper & Macdonald 2001). However, subjective location of the edge has become ubiquitous and many researchers applied this approach to complex boundaries (e.g., (Saracco & Collazo 1999); Adrian Weber, UBC, pers. comm.⁴). Alternatively, the lack of study on complex boundaries may have been because it was too difficult to establish where an edge was located.

Quantitative techniques using rates of change to delineate boundaries were introduced many years ago (Womble 1951), but were only adapted to ecological data in the early parts of the last decade (Fortin 1994; Jacquez et al. 2000). These techniques have been elaborated to use quantitative and categorical data that are arranged in regular and irregular patterns (Fortin & Drapeau 1995). Other techniques related to traditional clustering algorithms also created

⁴ Sadly, Adrian Weber passed away while he was conducting his PhD thesis. His research had an important component relating to dispersal of western redcedar seeds from a cedar dominated stand into a western hemlock-amabilis fir stand.

boundaries by grouping like entities (or plots) together, thereby creating boundaries between groups. Spatially constrained clustering via agglomerative hierarchical clustering limits the possibility of two plots being clustered together unless they are spatially contiguous and can be modified for better realism using a k-means algorithm (developed in Legendre (1986) and used in Legendre & Fortin (1989)). Both of these techniques were originally developed earlier in other fields, but were only adopted recently in ecology (Legendre & Fortin 1989). Other techniques that have been broadly used include moving split window (with one-dimensional data), edge detection in image analysis (with abundant, regular raster data), and fuzzy set modeling (with abundant data). Jacquez et al. (2000) provide a review of the various techniques for boundary delineation including much more detail than presented here.

1.3.2.2 Path Analysis

Traditional methods for inferring causal structures in ecological systems have been via experimental manipulations (Fisher 1926). Many, if not most, ecological questions are unanswerable using inference from manipulations due to several factors. First, large scale, landscape-related questions cannot be replicated easily and therefore cannot be analyzed via experimentation (Hargrove & Pickering 1992). Second, some questions are, by their nature, unable to be manipulated, such as how do wildfires and controlled burns differ in their ecological impact? Third, most ecological phenomena (e.g., population cycles in rodents) are caused or influenced by multiple factors and multiple scales which are often too complicated to manipulate (Hilborn & Stearns 1982; Ulanowicz 1997). Furthermore, it is logically (and mathematically) flawed to decompose a complex phenomenon into its component parts to understand the phenomenon because of the interactions between factors occurring over several scales simultaneously. There are some empirical examples of this limitation (e.g., snowshoe hare cycles; the failure of developmental biology to translate the entire sequenced genome of the adult nematode into the development of an organism (Lewin 1984)).

Some ecologists and biometricians claim that the only means of inferring causal structures is via experimentation. However, over 70 years ago, concurrent with Fisher, a geneticist demonstrated that there were alternate ways of explaining (viz. supporting a hypothesized causal structure) without manipulation (Wright 1921). This was referred to as path modeling. Path modeling generally begins with creation of a path diagram with single headed

arrows representing asymmetrical relationships. The hypothesis is subjected to data using a variety of measures of relative and absolute fit (see below—multiple hypothesis testing (Shipley 2000)). Path modeling has been criticized based on the notion that “one cannot prove causation”. Clearly, statistical support for a path model does not prove its causal structure because it is simply an hypothesis⁵. Rather, support for an hypothesis is increased by failure to disprove it; the level of support is a function of how often it is supported and against what it is compared (within a multiple hypothesis framework).

The relationship between correlation and causation has been largely ignored in statistics. However, in contrast to the notion that correlation does not imply causation, correlation implies *unresolved* causation. (There is a small set of cases for which this is not true, specifically those that are time ordered, e.g., Tuesday always follows Monday ($R^2=1$), but this does not imply any causation). Thus a statistical association between two variables (e.g., A and B) indicates one of three scenarios: 1) A causes B, 2) B causes A, or 3) a third (or more) variable(s) is (are) a common cause of A and B. One of the explicit goals of path analysis is to resolve this correlation structure using a combination of logical possibilities and partial correlation analyses.

Path models represent causal relationships, rather than just associations, by two mechanisms⁶. First, external logical information about the functioning of a process can be used. For example, if an association between rain and mud abundance is detected, it is clear that the mud did not cause the rain to occur. In some causal path (i.e., direct or indirect), rain was the cause of the mud. Second, in cases where external information is unavailable or inconclusive, the path model itself may have sufficient information that precludes misdirecting the relationship (Shipley 2000). Using multiple structured covariance and partial covariance analysis, support for a causal path may be unequivocal (Shipley 2000).

In addition to testing causal relationships, another benefit of using path models is the ability to test for direct vs. indirect relationships. Direct relationships are those in which the

⁵ Similarly, statistical support for a result in an experimental system does not prove the causal structure either.

⁶ I refer to Shipley's (2000) functional definition of causality: a relationship between events or classes of events (i.e., variables) that possesses the properties of asymmetry, transitivity, and the Markovian condition. I do not imply by the phrase “causal relationship”, that there is a 1:1 perfect cause and effect; nature can produce partial causes. Some authors have used the phrase “antecedent determinants” (e.g., Kimmins, 1997) and I view these as functionally synonymous.

association between two variables does not depend on any other modeled variable. For instance, light may have a direct (positive) influence on seedling abundance by providing adequate growth conditions for germinants to grow into seedlings. Light may simultaneously have an indirect (and negative) relationship on seedling abundance, mediated through the abundance of understory vegetation that competes with the seedlings. The inferential difference between these two types of relationships between light and seedling abundance may be important for prediction, understanding, and explanation. Without path analysis, a significant relationship between light and seedling abundance would be imprecise. The traditional means to account for this uncertainty was to explicitly manipulate vegetation abundance or to remove the variation in vegetation abundance from the study.

Numerous ecological studies have used path analysis in a broad range of applications (Schemske & Horvitz 1988; Farris & Lechowicz 1990; Kingsolver & Schemske 1991; Mitchell 1992; Wootton 1994; Grace & Pugsek 1998; Shipley & Lechowicz 2000; de Blois et al. 2001). These have been successful attempts to use this analysis technique; however, some detractors have demonstrated its shortcomings. In a long term experimental study on the effects of 2 species of rodent on desert vegetation, results from traditional analyses were compared to results from path analysis using the same data (Smith et al. 1997). The authors concluded that the two analyses resulted in different conclusions, with the traditional analyses being the correct ones. In direct response to this study, Grace and Pugsek (1998) demonstrated the methodological errors used in the previous critique (Smith et al. 1997), as well as pointing out that the expectations of path analysis were not appropriate. Furthermore, several studies have demonstrated that improper use of path analysis may have lead to many improper conclusions (Petraitis et al. 1996).

1.3.2.3 Multiple Hypothesis Framework

Since the late 19th century, the use of multiple working hypotheses for understanding the processes of interest has been advocated (Chamberlain 1890; Lakatos 1978; Hilborn & Mangel 1997). More recently in ecology, the realization that many different hypotheses may be true in different locations has begun to eliminate the strict use of H_0 and H_a (the standard null and alternative hypotheses). Consequently, different statistical frameworks have been developed (Bayesian analysis (Sit & Taylor 1998)) or created (Akaike Information Criteria) to work with

multiple hypotheses (Akaike 1973; Burnham & Anderson 1998). These different techniques either allow hypotheses to grow and change as new data are accumulated (Bayesian (Sit & Taylor 1998)) or put weight on alternative hypotheses (AIC), analogous to quantifying our degree of belief in the correctness of a hypothesis. In a simple system, or a highly reduced system, traditional hypothesis rejection can occur within these frameworks by having our degree of belief in a given hypothesis approach one (i.e., there is 100% support for one of the hypotheses). Thus, these approaches reduce to the traditional hypothesis falsification (Popper 1979) when the degree of belief is strong. In general, however, each hypothesis within the multiple hypothesis framework will have a non-zero numerical weight. In addition, testing spatial hypotheses via experimentation is plagued by having extremely low power (Steinberg & Kareiva 1997). Indeed, it has been suggested that the only way to understand spatial patterns in field-based studies is through specific models and their predictions (Steinberg & Kareiva 1997). Unfortunately, the lack of theoretical models for spatial processes severely hampers much of this work.

1.3.3 Natural Disturbance and Forest Management

1.3.3.1 The Natural Disturbance Paradigm

The ND paradigm provides a basis for a coarse-filter management strategy to maintain biodiversity and ecosystem function. It has been discussed as the basis for management plans (e.g., MacDonald & Coates 2002; Perera et al. 2003) and is being included in forest management plans or policies (e.g., Ministry of Forests & Ministry of Environment 1995). It uses the following logic applicable at all spatial scales of NDs:

- Premise 1: NDs are agents that kill trees and may create early seral communities when severe, and they are ubiquitous
- Premise 2: forest harvesting kills trees and is, thus, similar to NDs
- Premise 3: organisms are adapted to the characteristics of the local ND regime
- Deduction: in order to maintain organisms and ecosystem function, forest harvesting can emulate NDs as the agent of mortality since we are partially eliminating NDs from the landscape.

The premise that organisms are adapted to the ND regime characteristic of an area is key to the paradigm (Cissel et al. 1998; DeBano et al. 1998; Bergeron et al. 1999b; Parsons et al.

2000). While there are few explicit tests of the validity of this assumption, the existence of many species with adaptations to early seral communities lend support to the premise (Agee 1993). For instance, numerous tree species are shade intolerant and appear to almost exclusively regenerate after fire or other major stand replacing disturbances (e.g., trembling aspen [At], lodgepole pine [Pl] (Edmonds et al. 2000; Brown & Smith 2001)); numerous wildlife species increase in abundance in early seral stage forests (Steventon et al. 1998; Smith 2000); and numerous herbaceous plant species are most commonly seen after fires (Brown & Smith 2001). If these life history strategies are used as the sole basis for judging the importance of early seral forests, the logical conclusion is that any disturbance that recreates appropriate early seral conditions will be adequate for these species.

Clearly, there are problems with the proposal that harvesting can emulate natural disturbance (Franklin et al. 2002). Numerous wildlife species are adapted to the presence of standing dead wood that results from many natural disturbances. For instance, many bird species are bark gleaners that feed on the insects that colonize burned forest soon after the fire (e.g., nuthatches, woodpeckers (Hutto 1995)). Unfortunately, the relationship between fire caused tree mortality and fauna is not simple. By far the most useful types of dead trees are those with large diameter with high standing longevity (Smith 2000). These features are not present in conventionally harvested stands (though they are a component in variable retention harvesting) and so cannot confer the same benefits.

There are several reasons why wildfires are usually the primary disturbance agents of interest in the natural disturbance paradigm. First, much of the theoretical basis for this paradigm came from studies where forest fires are ubiquitous, such as Australia (Attiwill 1994a), the Canadian boreal forest (DeLong & Tanner 1996) and the Sierra Nevada. Second, wildfires are seen as the most catastrophic type of natural disturbance, often creating heavy tree mortality over large areas, and are generally the most visible (Johnson et al. 1998). Third, with characteristics such as near 100% tree mortality, periodicity on the order of 50 to 300 or more years, and reversion of the stand to an early seral stage, wildfires have some quantitatively similar features to clearcuts and are the mostly likely ND type for even aged forest management to emulate (Andison & Marshall 1999; Sullivan et al. 1999; Bergeron et al. 1999a; Bergeron et al. 1999b). One common thread in each of these studies is the need to estimate the natural range

of variability—the NRV (Cissel et al. 1998; Moore et al. 1999; Swetnam et al. 1999; Sullivan et al. 1999; Stephenson 1999).

Understandably, there is much opposition to adopting the ENFD paradigm and to basing management on the NRV of fires. For instance, researchers have claimed that historical fire frequencies are so variable that mean values (e.g., 80 years) can not be used as a basis for ND management to emulate (Andison & Marshall 1999; Bergeron et al. 1999b). Other warnings emphasize that one of the critical features of all NDs is that they leave dead standing or downed trees, features that have been largely absent in human disturbances (Lindenmayer 1995) and that can not be as abundant in harvests as in natural disturbances because of the removal of wood. Furthermore, only recently has there been explicit realization (within this context) that fires are not the only disturbances in forested landscapes and other types must be addressed and included in land management (Bergeron et al. 1998; McCullough et al. 1998). Overall, several studies indicate that forest harvesting mimics NDs poorly for a number of ecological values (Sturtevant et al. 1996; Niemela 1999; Stepnisky & Schmiegelow 2001). To critically examine and understand the strengths and limitations of using the ND paradigm as a basis for forest management, however, the underlying assumptions and the characteristics that describe NDs must be outlined and knowledge gaps must be identified.

A further problem with the ENFD paradigm is that it has often been applied aspatially. This leads to several problems. First, many faunal species use several different seral stages of forests on daily, seasonally, or lifetime schedules (e.g., Gates & Gysel 1978; Haila et al. 1994). Consequently, it is not simply which stages are present, but how they are related spatially to one another. Second, this paradigm implicitly takes a management defined “landscape” perspective because it refers to proportions of an area in each given seral stage (Ministry of Forests & Ministry of Environment 1995). While the management level “landscape” is a scale that appears important to humans, all organisms perceive the scale of the environment based on their body size (Peters 1983). Thus, the “landscape” as defined in this way is only a subset of the relevant scales for organisms.

The most common characteristics used to describe a given disturbance fall into three categories: spatio-temporal, magnitude of impact, and synergisms (Pickett & White 1985). Subdivided, spatio-temporal characteristics include frequency, return interval, rotation period, predictability, distribution and area or size. Magnitude characteristics are intensity and severity.

Synergism refers to the propensity for one type of disturbance to lead to another, such as severe insect outbreaks leading to fires (McCullough et al. 1998). While these are essential elements of an ecologically based management strategy, they do not explicitly incorporate the inherent variability *within* and *between* forest stands that have been subjected to a ND event. In particular, the boundary zones are virtually non-existent and edges are assumed to be linear in many approaches to ecosystem management.

To date, implementation of stand-level variation based on NDs has involved three strategies: the use of wildlife tree patches (Eberhart & Woodard 1987; Ministry of Forests & Ministry of Environment 1995; Morgantini 2001), the use of different retention levels (North et al. 1996; Kohm & Franklin 1997; Chambers et al. 1999) and silvicultural techniques of manipulating stand density and planted species. Consideration of boundaries has largely been absent from management designs. Not only has there been very little attempt to characterize the real variability in NDs and their edges; there has been an implicit assumption that ND boundaries are hard. Indeed, in a recent special issue on the historical variability of NDs (Parsons et al. 1999), the concept of boundary variability is absent. Based on a range of descriptions from the Picket and White definitions (1985), through BC Ministry of Forests (1995) to recent examinations of the ND paradigm (Parsons et al. 1999), one might conclude that emulating ND would be as simple as choosing a single level of retention in a given harvest block. Fortunately, with the addition of variable retention and other types of dispersed retention in some locations, this tendency towards spatial simplification is on the decline (Franklin et al. 2002).

One possible reason for the lack of implementation of stand boundary variability is the lack of knowledge about whether there is indeed substantial variation. Are the boundaries between intact forests and disturbed areas purely one-dimensional and linear? Alternatively, is there measurably greater heterogeneity in vegetation and live and dead structure at the boundaries? Are there measurable ecological features that are unique within these boundary zones?

1.4 General Methodology

Included here are general methodological components that are not elaborated in the data chapters.

1.4.1 Study Area

Research was conducted in the Arrow Lakes and Kootenay Forest Districts (AFLD and KFD), in south central BC. This region is characterized by high mountains with steep to shallow slopes throughout. The forests in this area have the highest diversity of tree species in BC (Meidinger & Pojar 1991). Western redcedar (*Thuja plicata* Donn ex D. Don), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), white X Engelmann spruce hybrids (*Picea engelmannii* x *P. glauca*), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) are the dominant climax species throughout the forests. Lodgepole pine (*Pinus contorta* Dougl. ex Loud.) occurs as an early seral stands throughout this area. Other common tree species include western larch (*Larix occidentalis* Nutt.), and Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco)(Burns & Honkala 1990). In this study, I sampled forests in the Interior Cedar Hemlock moist warm and the Engelmann Spruce Subalpine Fir wet cool biogeoclimatic subzones⁷ (ICHmw2, ESSFwc1, and ESSFwc4)(Meidinger & Pojar 1991). These three biogeoclimatic subzones are contiguous and usually occur in immediate proximity to one another on mountain slopes. According to the biodiversity guidebook (Ministry of Forests & Ministry of Environment 1995), they are characterized by stand replacing fire disturbance regimes, with a return interval ranging from 150 years to 400 years (NDT 1 and 2, rare or infrequent stand initiating events).

1.4.2 General Site Selection

All disturbance events investigated took place between 1993 and 1997. This reduced time as a factor involved in creating variability. Furthermore, no sites contained large (>400 m²) edaphic gaps where trees could not grow, since trees and tree mortality were the focus of this study. All MPB outbreaks that occurred between 1993 and 1996 in the ALFD and that had a reported severity >30% and a reported size >2 hectares were sampled. In addition, all fires during this period that had large areas without salvage logging were sampled. These stands had the following characteristics:

- Mature stands (60 years < tree age at DBH < 150 years)
- 15 cm < DBH < 30 cm

⁷ The term "zone" is used in this thesis to represent a fine scale area of land that is part of the description of boundaries (see Figure 1.1). The use of the term "zone" in the context of the BC Biogeoclimatic Ecosystem Classification is the only departure from the boundary use of this term. These two uses should not be confused.

- Southerly aspect slopes (97° to 256°)
- Slope angles from ~10° to 30°
- Site series: #3 (most common), #1 or #5, representing moderately dry to mesic conditions
- Disturbance size: 20 ha to 200ha (included the largest fires in Region)
- MPB:
 - >55% Pl in the canopy
 - 1150 m < Elevation < 1550 m.
- Fire:
 - 1400 m < Elevation < 1900 m.

One problem with examining fire edges is that many fires have been subjected to fire suppression. I chose to study areas of the fires that had the least evidence of active fire suppression based on absence or low frequency of red fire suppressant, cut trees, and Pulaski fire guards. I concentrated on the sides of the fire event, rather than the upper end because all visited fires had extensive fire suppression at the upper ends.

Within the constraints listed above, all transects were located randomly within a given disturbance event. Except for two fires that had two transects each, located >1 km apart, only one transect was placed in each disturbance event.

1.4.3 Data Collection

The sampling design involved contiguous 5m X 5m square plots placed in transects that ranged in width from 40m to 60m and in length from 60m to 180m (Figure 1.1). To obtain larger scale plots, 4 (10m X 10m) or 16 (20m X 20m) adjacent 5m X 5m plots were merged. Every 10mX10m plot contained a 10m² circular vegetation/regeneration plot at the center. The transect length was defined by the character of the boundary being measured. The two dotted lines depict a hypothetical example of the calculated inner and outer limits of the boundary zone delineated in Chapter 2. Successional trajectories for the three zones depicted in Figure 1.1 are calculated in Chapter 4.

1.4.3.1 General Variables of Interest

A summary of the variables of interest and plot sizes are listed in Table 1.1. More detailed use of variables is described in the methods section of each chapter.

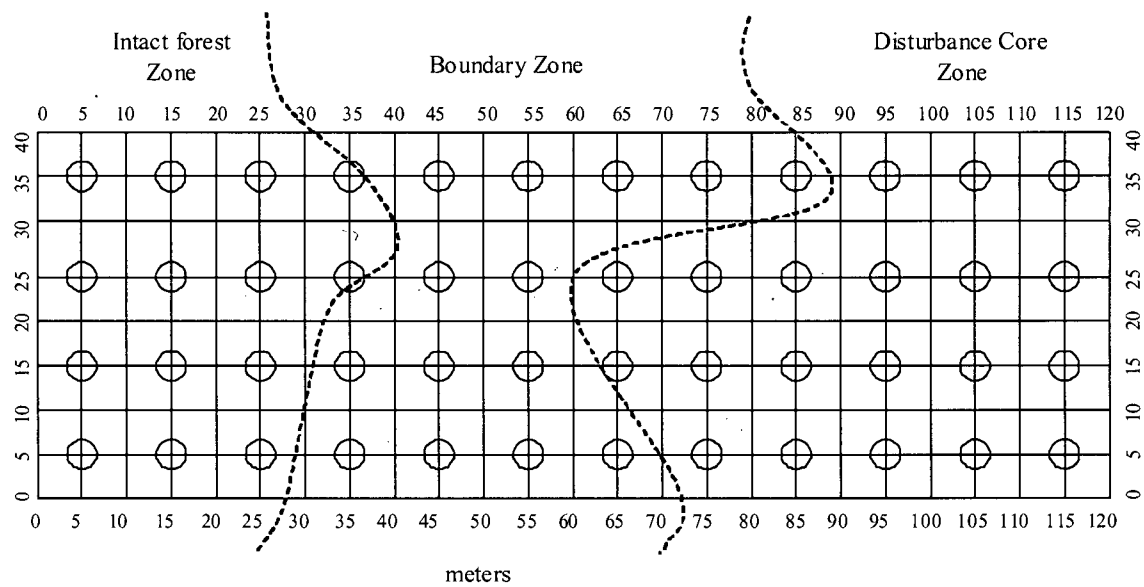


Figure 1.1. Design of sampling transect with an example of a soft boundary delineated by inner and outer boundaries showing the intact forest zone, boundary zone and disturbance core zones.

Table 1.1 Summary of sampled variables. Techniques for all measurements were taken from BC Ministry of forests field manuals (Armleder et al. 1992; Meidinger et al. 1998)

Characteristic of interest	Chapters used in	Plot type	Measured variables
Trees (>10 cm at DBH)	Ch. 2,3,4	5m X 5m plots, or aggregated to 10m X 10m or 20m X 20m plots	• Species • Diameter at breast height (DBH) • Height • Determine agent of mortality and confirm if agent of interest (e.g., MPB)
Tree sapling disks (2 cm< diameter at root collar <7.5 cm)	Ch. 4	1 sapling (50cm to 5m tall) per 10m X 10m plot	• Tree disk taken at root collar
Understory Vegetation	Ch. 4	10 m ² circle	• Percent cover by species (all species >0.5% cover), in each of the A, B1 and B2 layers
Natural regeneration (height >5 cm and < 50 cm)	Ch. 4	10 m ² circle	• Count by species
Environmental Variables	Ch. 3	Once per 10mX10m plot	• Elevation, Slope, Aspect

Chapter 2 Structural Properties of Natural Disturbance Boundary Zones: Implications for Landscape Heterogeneity⁸

2.1 Introduction

Boundaries between landscape elements (e.g., two plant communities) are features with large rates of ecological change through space and high degrees of heterogeneity (Wiens et al. 1985; Hansen & di Castri 1992). Their ecological influence may be disproportionate to their area on the landscape (Holland et al. 1991). The body of research on “edge effects” on plants describes part of the importance of boundaries as a landscape feature (Laurance & Yensen 1991; Chen et al. 1992; Matlack 1993b; Voller 1998).

The problem with boundaries, in general, is that they are complex spatial phenomena whose description changes dramatically depending on the scale of analysis (Gosz 1993; Fortin 1999; Fortin et al. 2000). Natural disturbance boundaries are often depicted in a polygon-based land-use map as a series of linear, one-dimensional features dissecting the landscape. Whether they are actually linear and one-dimensional or are two-dimensional landscape features that have unique ecological characteristics is often not known. In reality, boundaries can be depicted and can function as one dimensional and two dimensional phenomena, depending on the spatial scale. To resolve this dimensional conflict, their characteristics need to be studied at multiple scales (Gosz 1993; Peterson & Parker 1998). Furthermore, the functioning of the boundary will depend on the spatial scale of the process of interest (Forman 1995; Turner et al. 2001). Boundaries that occur at the periphery of natural disturbances have functions on many scales; the simplified depiction on landscape-level maps may not sufficiently capture ecological processes that happen at stand scales. Before understanding forest boundaries, however, the variety of boundaries that occur in landscapes must be objectively described.

Natural disturbances are agents of tree mortality and have become a key ecological focus of forest management. Some ecologists have suggested that forest management use these natural processes as a template for stand and landscape planning. Indeed, the “natural disturbance

⁸ All data chapters (Chapters 2 to 4) are written as stand-alone manuscripts with two minor alterations: there are no separate abstracts or literature cited sections.

paradigm” has been ubiquitous in forestry literature for at least ten years (Attiwill 1994b; Galindo-Leal & Bunnell 1995; Christensen et al. 1996; Bergeron & Harvey 1997) and has formed a basis for sustainable forest practices in some regions for several years (Ministry of Forests & Ministry of Environment 1995). Traditional harvesting techniques, however, have little in common with fires except for creating a light environment suitable for the regeneration of shade-intolerant species (Franklin et al. 2002). For instance, the creation of landscape homogeneity has been a characteristic of past forest management and is not representative of natural fires (Turner et al. 1994). Furthermore, examining fires as the only source of natural patterns is equally simplifying given that other natural disturbances occur.

Fires and insect outbreaks are characterized by spread behaviour that can be modeled conceptually or mathematically (Rothermel 1972; Barbosa & Schultz 1987; Turner et al. 1989; Anderson & Cumming 2001; Andrews & Bevins 2002). This behaviour suggests that disturbance events have sites of origination, move outwards non-randomly, and end up by slowing down (fires) or encountering dispersal limitation (insects). This slowing or ending of the spread may or may not happen rapidly in time, thereby creating a boundary that may or may not be “abrupt” in space (Forman 1995). While the processes and mechanisms underlying the spread of fires and insects are different, these different disturbance types share some common features, indicating that the boundary morphology of these disparate types of disturbances may be similar.

Only recently have adequate tools been available to appropriately describe boundaries (Kent et al. 1997; Fortin et al. 2000). Past attempts to describe them have largely addressed the problem of boundary delineation (Fortin 1997; Hall & Maruca 2001). This study focuses on methodologies for describing boundary zones—the two dimensional area that contains intermediate characteristics between the most severe parts of a disturbance event and the area immediately outside the event. Boundary zones are a particular type of transition area (*sensu* Kent et al. 1997), and are differentiated from edges (one-dimensional features) that have been described around the perimeter of a clear cut or an area of land use change.

The primary objective of this study was to examine, delineate, describe and compare the spatial patterns of the boundary zone created by fires and mountain pine beetle (MPB). Here, a boundary zone is defined as the part of the landscape that occurs between the peak disturbance severity and the surrounding areas that have little or no mortality due to the disturbance in question. Several specific questions are addressed. Can spatially complex boundaries be defined

and delineated at the forest stand scale? Can spatially constrained clustering be used to objectively describe complex boundaries? Do NDs create soft boundaries? In other words, do they create two-dimensional areas of land rather than linear entities (this will be a question of scale)? What are the width, steepness, sinuosity, and heterogeneity of the boundary zone? Is the boundary zone more heterogeneous than the intact forest or disturbance core? Are these values a function of the plot size used (5m, 10m, and 20m)? Do MPB and Fires differ in their spatial patterns at the boundary? The implications of the answers to these questions for forest management and our descriptions of the natural landscape are discussed.

2.2 Methods

2.2.1 Field Sampling

2.2.1.1 Study Area

Research was conducted in the Arrow Lakes and Kootenay Forest Districts, in south central BC within three biogeoclimatic subzones (ICHmw2, ESSFwc1, and ESSFwc4 (Meidinger & Pojar 1991)). These subzones are contiguous on mountain slopes. Sampled sites had slope angles ranging from $\sim 10^\circ$ to 30° . All MPB sites were dominated by lodgepole pine (*Pinus contorta*) and fire sites were dominated by lodgepole pine, subalpine fir (*Abies lasiocarpa*), white X Engelmann spruce hybrids (*Picea engelmannii* X *glauca*), or Douglas-fir (*Pseudotsuga menziesii*). According to the British Columbia biodiversity guidebook (Ministry of Forests & Ministry of Environment 1995), these zones are characterized by stand replacing fire disturbance regimes, ranging from 150 years to 400 years (NDT 1 and 2, rare or infrequent stand initiating events).

In the summer of 2001, seven two-dimensional sampling transects were established in five different fires (sites F12 and F20, and F17 and F21 were from the same fires, however, the two transects were separated by at least 1 km from each other). All disturbances occurred between 1993 and 1997. The fires were all lightning caused, had extensive areas that were not salvaged, were amenable to being sampled (i.e., no slopes $> 50^\circ$), occurred at elevations between 1400m and 1900m, and were in the province's fire database (Protection Branch 2001). All fires had had active fire suppression efforts; however, site selection within each fire was constrained to sites where there was no or minimal evidence of local suppression efforts (e.g., Pulaski lines

[fire guards], red retardant embedded in downed wood, evidence of trees cut during the fire). Fire boundaries examined in this study were along the side flanks of the fire event that moved up the slope and were located horizontally across the mountain slope to avoid heavy suppression efforts at the front of the fire. The eleven MPB sites had the following characteristics: mature stands (60 years < tree age at DBH < 150 years); canopy trees at least 20 cm, DBH; southerly aspect slopes (97° to 256°); and, elevation between 1150m and 1550m. All sites that were within the study area and that were recorded as "severity 3" (>30% overstory mortality) in the forest health database (Pacific Forestry Centre 2001) that were within the study area and biogeoclimatic zones were sampled once. In preliminary visits to sites of lesser severity, it was not possible to find areas of MPB mortality while doing ground surveys. Often, a large area was mapped with variable severity and was labeled "severity 1" or "severity 2" which would indicate a high level of spatial heterogeneity. MPB stands were overall of similar character due to specific habitat selection by the insect disturbance (mature lodgepole pine); however, the secondary tree species and understory vegetation were not necessarily similar throughout.

2.2.1.2 Sampling Transects

All sampling occurred using 2-dimensional sampling transects that ranged from 60m to 170m long and 40m to 60m wide (Table 2.1). The two transects that were wider than 40m had low mortality (M09) and very low tree densities (F17). Placement of transects was done in a three-step process. First, MPB outbreaks or fires, which occurred within the study area during the years 1993-1997, were found using fire and insect databases (Pacific Forestry Centre 2001; Protection Branch 2001). Several spatially random points were located within each outbreak or fire using a GIS and random point generator (Environmental Systems Research Institute 1999). Second, one of the random points was visited and assessed for the following: was there actually tree mortality, and was the site free or virtually free of fire suppression (red fire suppressant stain on wood and presence of cut trees). When these conditions were not satisfied, a second (and third, etc.) random point within that disturbance event was visited and the assessment was repeated until a random point that fulfilled these conditions was found. Third, a line perpendicular to the closest mapped boundary was examined on the ground for at least 500m or until evidence of the disturbance had virtually disappeared (i.e., no fire scarring, and no obvious clusters of MPB killed trees). In all but one cases (F12), continued sampling along the transect

outward from the disturbance did not cause reentry into more disturbed areas. For fires, this line was invariably along a contour line across the mountain slope crossing the side flank of the fire that had moved upslope. Finally, the transect was placed to encompass all edge conditions from the peak severity of the disturbance core to the intact forest (see Figure 1.1). Each transect had a field-estimated 20% of the plots inside the disturbance core and a field estimated 20% outside the disturbance (near zero tree mortality). The overall length and width of each sampling transect was determined by the variability of the stand being measured.

Each transect was sampled at a 25m^2 resolution (5m X 5m plots). All data analyses were performed on these 5m X 5m plots and were repeated on aggregates of 4 (10m X 10m) or 16 (20m X 20m) of these small plots to address multiple scales of spatial pattern. All trees >10cm diameter at breast height were measured.

2.2.2 Data Analysis

2.2.2.1 Boundary Delineation

A standardized measure of disturbance severity was used (Basal Area killed/[BA killed + BA alive]) for all boundary delineation and description. This measure was used so that the boundaries would be defined solely by the direct effects of disturbance on trees. To describe the boundaries and the zonation within the transects, I used a spatially constrained clustering (SCC) with the k-means adjustment (Fortin & Drapeau 1995) using the software BoundarySeer (TerraSeer 2001). SCC is a technique that creates hard boundaries between dissimilar features creating spatially distinct patches. The hardness or softness of a boundary is scale dependent: what appears hard at one scale may be soft at a finer scale. By providing a complete delineation of a study area, the patches generated can either represent spatial homogeneity or heterogeneity (Fortin & Drapeau 1995). Given that I was interested in measuring the width and shape of a boundary, the sampling transects needed to be completely delineated. Hence I used small plot sizes and SCC to capture any differences.

In SCC, formation of clusters using the dissimilarity matrix ($1 - \text{Euclidean distance}$) was constrained to only those plots that are contiguous, creating closed areas with hard boundaries. At each step, the most similar of all spatially adjacent sampling units, or clusters of sampling units, were merged, and coalescing continued until an optimal number of clusters was found using the goodness-of-fit statistic (Gordon 1999). A connectedness of 0.8 was used to minimize

single plot clusters (also see Hall & Maruca 2001). For large sample sizes like those that occurred with the 5m plots (~200 plots), there were often several local goodness-of-fit optima. I selected the strongest one where there was a clear, local optimum. Where several were equally good, I used the cluster number that minimized single plot clusters. This usually occurred above 10-15 clusters and below 25. For 10m plots, there was usually only one optimum. For 20m plots, there was often no optimum; 3 clusters were used as a default for 20m resolution.

2.2.2.2 Boundary Characterization

Using ArcView® geographic information system (Environmental Systems Research Institute 1999), distances between the lowest severity and highest severity clusters were measured (Figure 2.1). These lowest and highest severity clusters were identified at each site to represent areas inside and outside the disturbance, respectively. Clusters that were identified as high or low severity but were less than 400m² were rejected as being too small to represent the disturbance core or intact forest. Only larger, contiguous areas were used to represent these extremes of severity. To measure distances between the high and low severity clusters, all sampled plots that were within the cluster and that were adjacent to the cluster edge that was facing the opposite severity cluster were identified (Figure 2.1: white and black symbols). These plots create the inner and outer boundaries and are the basis of dividing the area into three zones: inside the disturbance (IN), outside the disturbance (OUT) and in the intermediate boundary zone (BZ). The distance was calculated between each plot center along this edge to the nearest plot in the opposite severity cluster. This process was repeated for both low and high severity cluster plots. In cases where there was more than one identified low or high severity cluster (a situation that arose often because of the inherent variability of the boundaries), up to four candidate clusters were selected (two inside the disturbance and two outside) to minimize and maximize the boundary width calculations (Figure 2.1). These two calculations are herein referred to as either maximized boundary zone (MaxBZ) or minimized boundary zone (MinBZ). All results use both of these calculations of boundary width. Due to small sample sizes (Fires: N=7; MPB: N=11), non-parametric statistical tests are used throughout to compare MPB with fire (SAS Institute Inc. 2000).

Sinuosity was calculated for both maximized and minimized boundary zones as the sum of two ratios: the ratio of the inner boundary length to the straight line inner boundary length

plus the ratio of the outer boundary length to the straight line outer boundary length (Figure 2.2). The lowest value sinuosity can take is 2 if both the inner and outer boundaries are straight. In cases where the inner and outer boundaries are identical (i.e., there is no boundary zone), the sinuosity is calculated as if there were two identical boundaries. In sites where the zone did not cross the entire transect, the straight line is calculated using a triangle (Figure 2.2).

To measure the heterogeneity in the boundary zones, within-zone variance of standardized disturbance severity was calculated for each of the three zones delineated by the spatially constrained clustering (outside the disturbance [OUT], inside [IN] and in the intermediate boundary zone [BZ]). These levels of variance are compared within and between disturbance types for both MinBZ and MaxBZ.

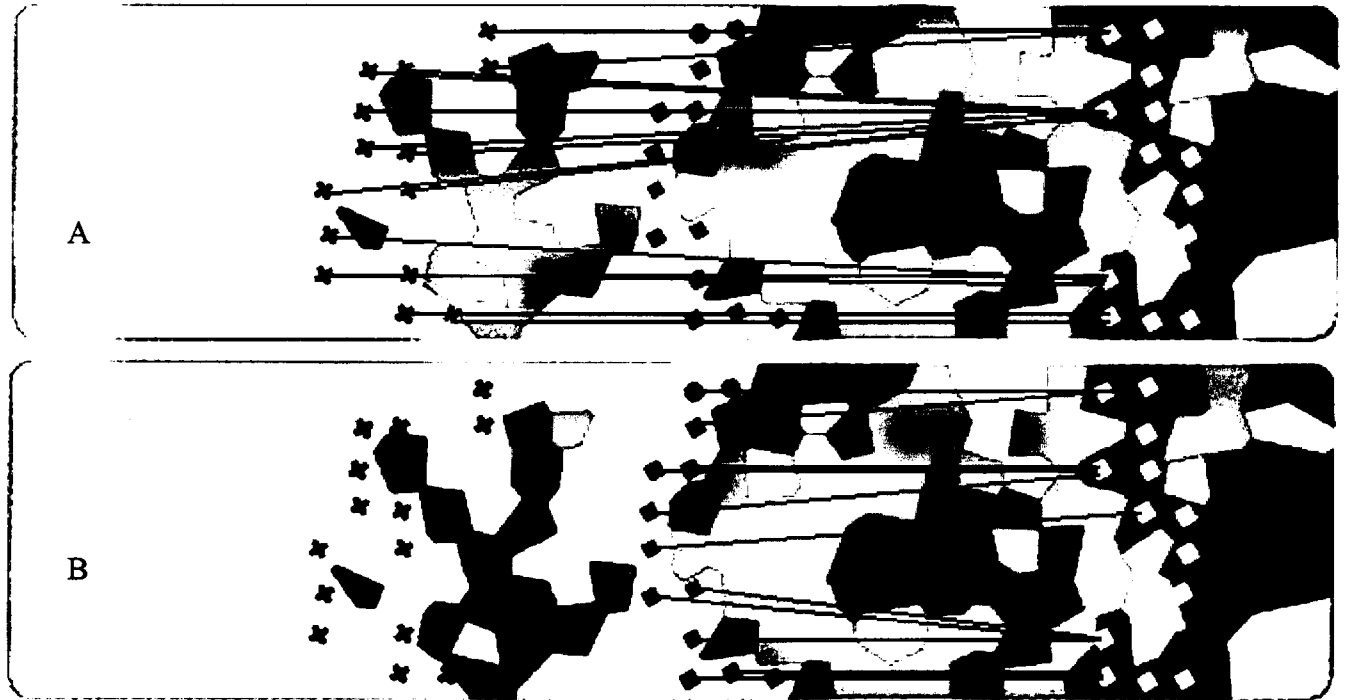


Figure 2.1. Methodology for identifying minimum and maximum severity spatial clusters and for calculating minimum boundary zone (MinBZ) and maximum boundary zone (MaxBZ) width. For clarity, only the distances from low severity plots to the nearest high severity plots are shown. A similar number of linear measures were identified from each high severity plot to the nearest low severity plot. Cluster colour ranges from white (0% mortality) to black (100% mortality). Symbol colour: White=peak severity clusters; black= minimum severity clusters; diamonds=minimum distance estimate; crosses=maximum distance estimate (where applicable). A. Maximum width estimate. B. Minimum width estimate.

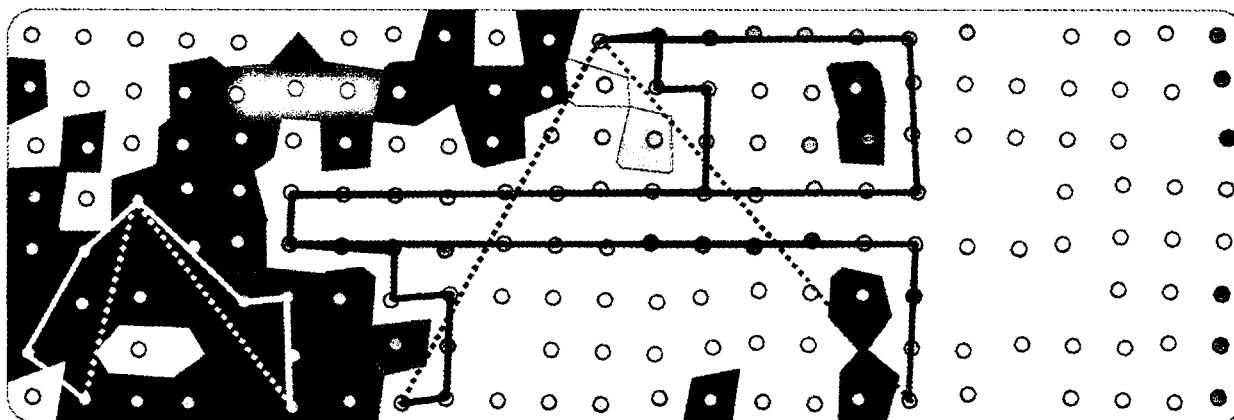


Figure 2.2. Sinuosity calculation for site M13, 5m plot. Sinuosity is calculated as actual boundary length divided by minimum boundary length for each inner and outer boundary. Lines would link closest plots; diagonals were therefore not used unless there were missing data and a diagonal move was the closest. Symbols: circles = 5m plot centers. Lines: solid = shortest possible boundary given the shape of the transect; solid = actual measured boundary; white: inner boundary; gray = maximum outer boundary; black = maximum outer boundary. Cluster colour ranges from white (0% mortality) to black (100% mortality).

Table 2.1. Summary and properties of sampled sites.

Site#	Type	Sampling Transect		# plots per site at			Disturbance	Reported disturbance
		Length	Width	each plot size				
		(m)		5m	10m	20m	year	Size (ha)
02	MPB	110	40	176	44	11	1995	24
03	MPB	100	40	160	40	10	1993	35
05	MPB	170	40	272	68	17	1995	133
06	MPB	120	40	192	48	12	1993	39
08	MPB	140	40	224	56	14	1995	59
09	MPB	120	50	240	60	12	1993	171
10	MPB	130	40	208	52	13	1995	62
13	MPB	120	40	192	48	12	1993	73
14	MPB	150	40	240	60	15	1995	75
15	MPB	140	40	224	56	14	1994	18
16	MPB	140	40	224	56	14	1994	48
11	Fire	120	40	192	48	12	1997	62
12	Fire	160	40	256	64	16	1994	77
17	Fire	100	60	240	60	15	1994	50
18	Fire	60	40	96	24	6	1994	6
19	Fire	100	40	160	40	10	1994	47
20	Fire	110	40	176	44	11	1994	77
21	Fire	130	40	208	52	13	1994	50

2.3 Results

Peak severity (as measured by BA killed/[BA killed + BA alive]) was significantly higher in the fires than MPB at all plot resolutions (Wilcoxon rank sum test; 5m: $p=0.02$; 10m: $p=0.006$; 20m: $p=0.002$). The magnitude of the differences in peak severity depended on the resolution of the sample unit (Figure 2.3). Severity was highest for both fire and MPB at the 5m resolution (0.97 vs. 0.77) and was lowest at the 20m resolution (0.89 vs. 0.43). The three spatial scales were significantly different for each MPB and fire sites (Kruskal-Wallis tests; MPB: $p=0.005$, Fire: $p=0.02$).

In spatially constrained cluster analysis, neither 5m or 10m plots showed a goodness of fit optimum with only 2 (or 3) easily demarcated clusters which would represent high, (intermediate) and no severity of disturbance (e.g., Figure 2.4). This resulted in more complex and convoluted boundary zones (Figure 2.5). The four example maps shown here give a selection of the 54 maps (3 resolutions X 18 sites) that were created to calculate boundary descriptions. All sites showed variability and had localized variation within the boundary zones. In the four examples, plots used for calculating boundary widths are also shown. For instance, in Figure 2.5A, the minimum distance was calculated as the mean distance from each of the white diamonds to its closest black diamond, and from each black diamond to its closest white diamond. The maximum distance was the mean distance from each of the white diamonds to its closest black cross and from each black cross to its closest white diamond. In this example, there is only one large cluster of suitable size ($>400\text{m}^2$) inside the disturbance. In cases where there were two suitable clusters inside and outside the disturbance, there are four possible distance calculations; only the minimum and the maximum distances are shown.

Boundary widths for MPB ranged from 5m (MinBZ at site M09) to 127m (MaxBZ at site M05), with MaxBZ means of 48m, 61m, and 51m (5m, 10m, and 20m plots, respectively, see Figure 2.6). Fire boundary widths ranged from 6m (MinBZ at site F19) to 107m (MaxBZ at site F12), with mean MaxBZ widths of 30m, 40m, and 51m (5m, 10m, and 20m plots, respectively). Mean MinBZ widths for MPB were 15m, 30m and 37m and for fires were 15m, 29m, and 51m for the three plot sizes. These large ranges indicate large variability within disturbance types and with distance estimation type. At all resolutions and both MinBZ and MaxBZ estimates, fire and MPB had similar boundary widths with the greatest difference occurring for the MinBZ at the

20m-plot resolution (Wilcoxon rank sum tests: MPB=37m, Fire=51m, $p=0.04$). Within each disturbance type, sampling unit resolution did not significantly affect boundary width for MaxBZs (MPB: $p=0.51$; fire: $p=0.06$) but was a highly significant influence on boundary width for the MinBZs (MPB: $p=0.005$; fire: $p=0.007$). (Sample sizes for 20m resolution are lower than adequate, but I include those data because the results are consistent with the other resolutions and 20 X 20m plots are a common size for forestry applications.)

At all sampling unit resolutions and for both MinBZ and MaxBZ widths, fires had steeper boundaries (Figure 2.7). Wilcoxon rank sum tests indicate that MaxBZ steepness at 10m and 20m-sampling units are significantly steeper for fires than MPB. Sinuosity was highest at 5m plot resolution and smallest at 20m resolution (Figure 2.8). Fire and MPB sinuosity was not significantly different for both MinBZ and MaxBZ ($p>0.25$). At the 5m resolution, MPB tended to have more sinuous boundaries as compared to fires.

In all situations (fires and MPB, at all resolutions), boundary zones showed the highest or equally high variability of tree mortality as compared to zones inside and outside the disturbances (Figure 2.9). This pattern was strongest for fires with the boundary zone accounting for the greatest variability at the 5m X 5m resolution (for MaxBZ) and at the 10m X 10m (for both MinBZ and MaxBZ). MPB only showed differences in variance between the three zones at 5m and 10m (only MaxBZ). MPB showed high variance inside the disturbance and in the boundary zones. In general, variance was lowest at the 20m resolution and boundary zones were most variable at the 5m resolution.

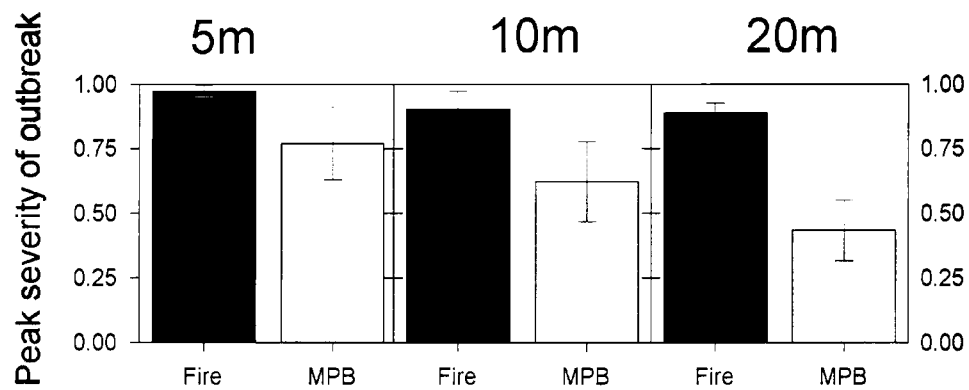


Figure 2.3. Peak severity of disturbance event based on the maximum severity clusters (BA killed/[BA killed + BA alive]). Black=Fires; Grey=MPB. Error bars indicate 95% confidence limits (see Table 2.1 for sample sizes).

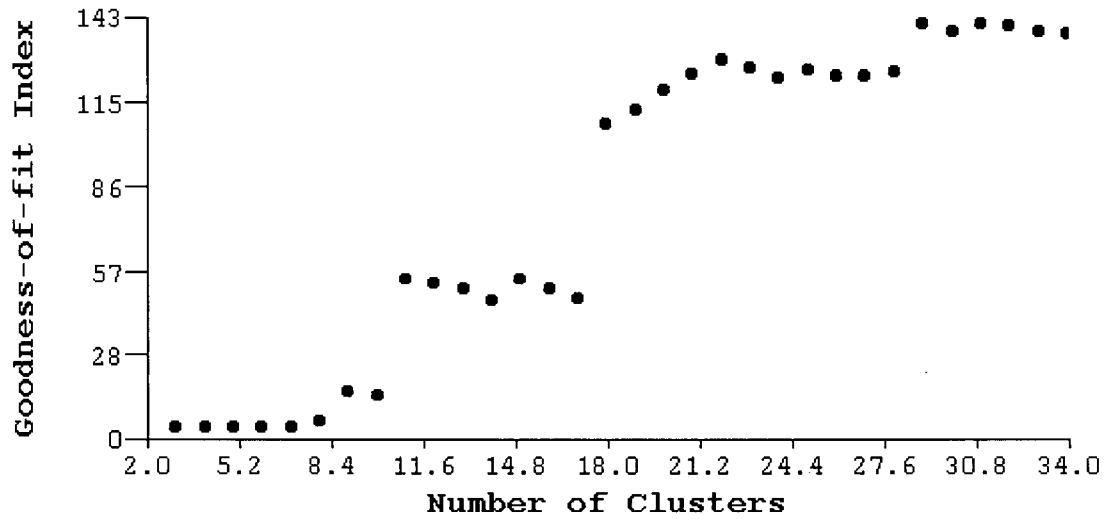


Figure 2.4. Sample goodness-of-fit graph. Site F12, 5m resolution, corresponding to Figure 2.5A. In this sample, 22 clusters were selected. Alternatively, 11 clusters could have been selected, but mostly single plot clusters were created.

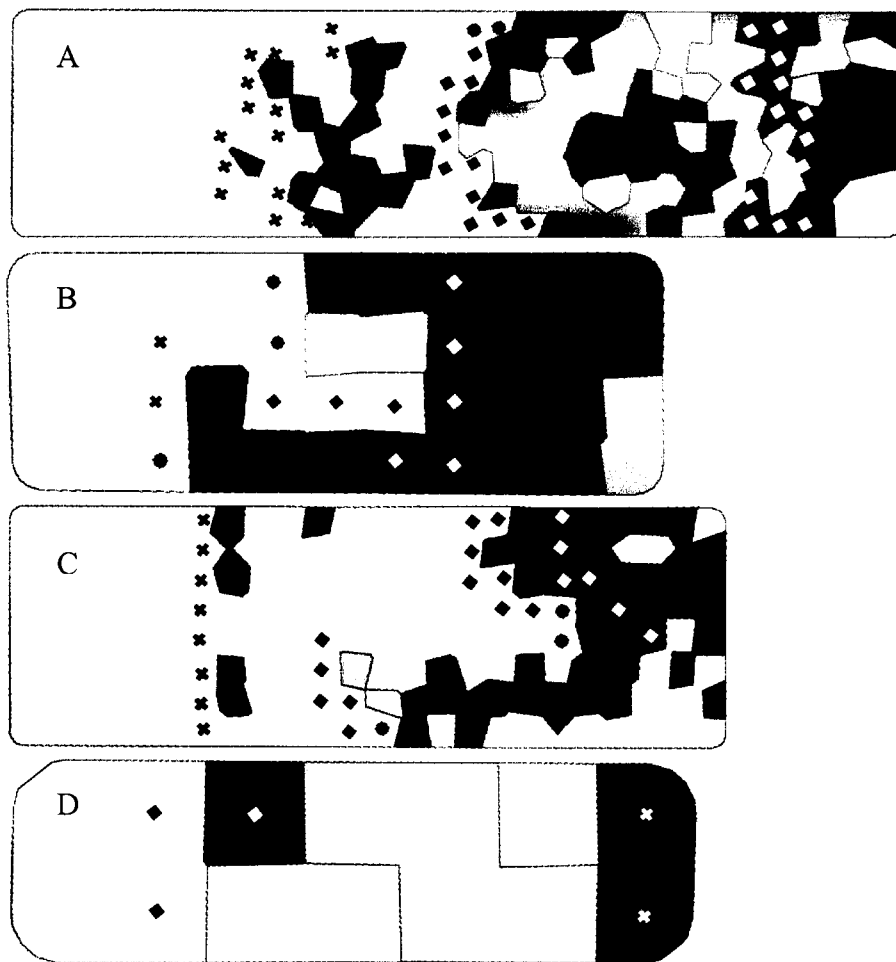


Figure 2.5. Cluster maps of four sites with points used for calculating distances. Cluster colour ranges from white (0% mortality) to black (100% mortality). Symbol colour: White=peak severity clusters; black=minimum severity clusters; diamonds=minimum distance estimate; crosses=maximum distance estimate (where applicable). Inner boundaries are represented as the line connecting black symbols; outer boundaries are the line connecting white symbols. A) Site F12, 5m plots; B) Site F20, 10m plots; C) Site M13, 5m plots; D) Site M16, 20m plots.

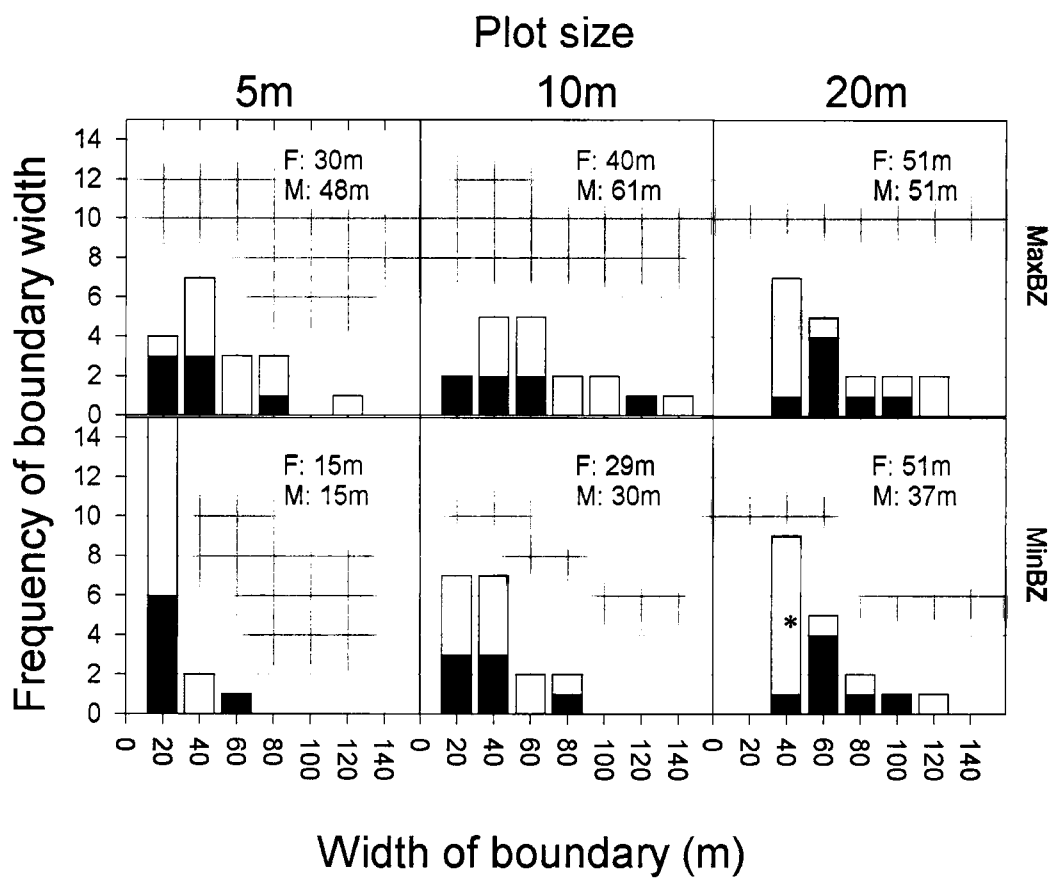


Figure 2.6. Histogram of boundary widths by plot size, disturbance type, and estimation type. Means are indicated on each graph. Black=Fires; Grey=MPB. Wilcoxon rank sum tests, *: $p < 0.05$.

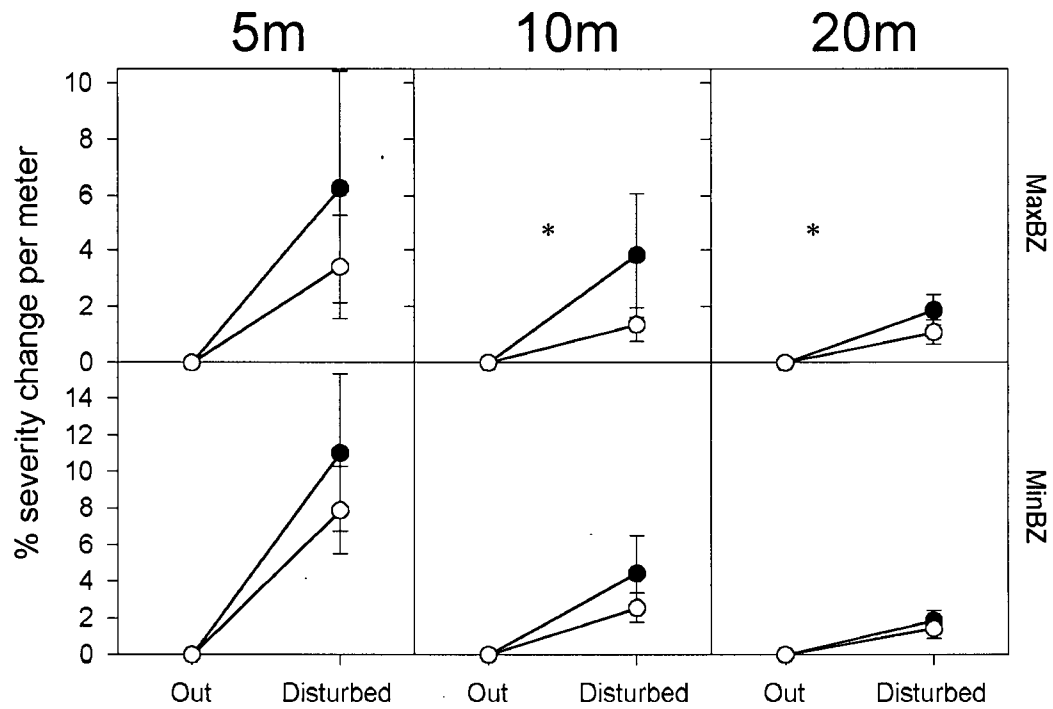


Figure 2.7. Steepness of boundaries. Black=Fires; Grey=MPB (units are % severity change per meter $\pm$ 95% C.I.). Wilcoxon rank sum tests, *: $p < 0.05$.

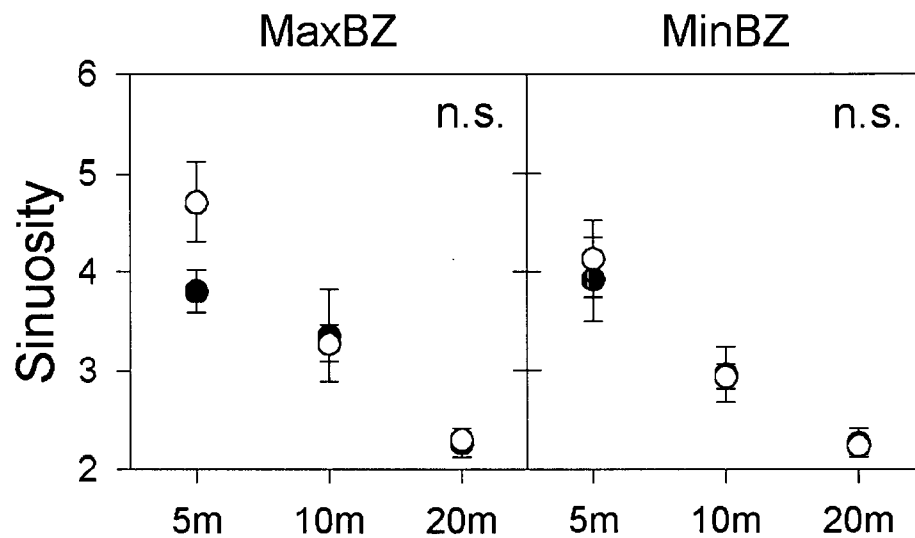


Figure 2.8. Sinuosity of boundaries. Black=Fires; Grey=MPB (units are inner boundary length/straight length + outer boundary length/straight length $\pm$ S.E.). Wilcoxon rank sum tests between fire and MPB, n.s.: $p > 0.25$.

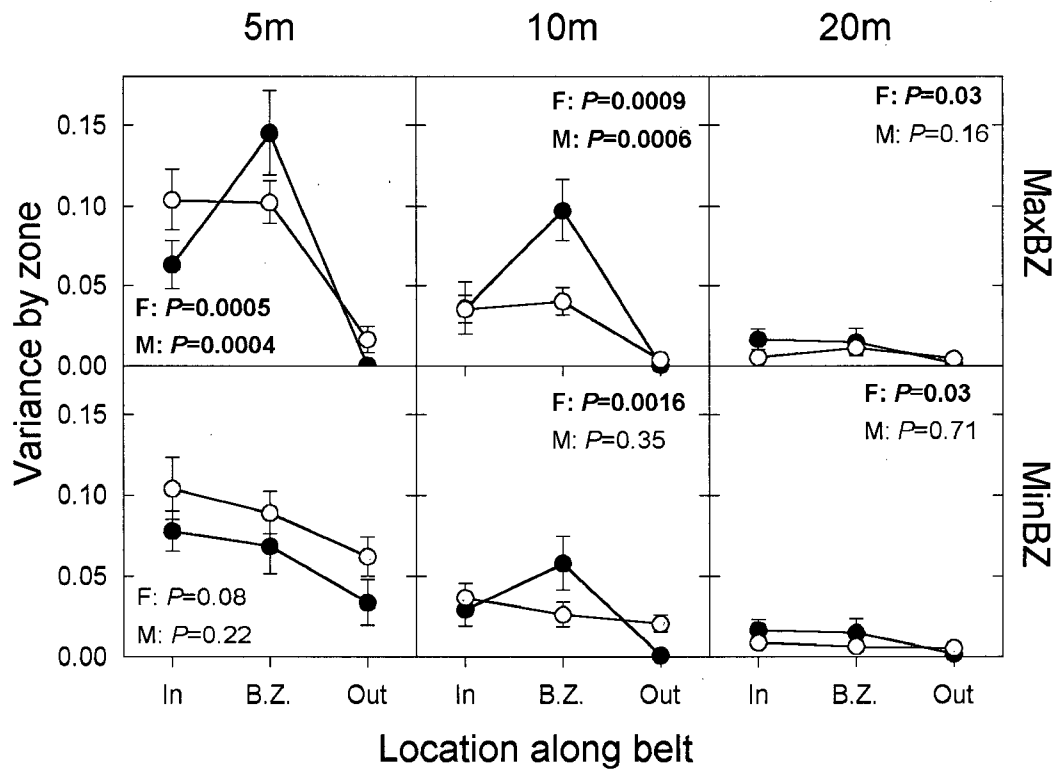


Figure 2.9. Between plot variance in severity within each of three zones: inside the disturbance, in the boundary zone (B.Z.) and outside the disturbance. See text for MaxBZ and MinBZ. Probability levels are shown comparing the three zones for fire and MPB (Kruskal-Wallis (SAS Institute Inc. 2000)).

2.4 Discussion

There are two primary results of ecological and management significance from these data: first, in terms of disturbance severity, the boundary zones are at least, if not more heterogeneous than the disturbance core; and second, mean boundary widths are 51m for both MPB and fire when calculated using a 20m sampling unit resolution.

Spatially constrained agglomerative clustering was determined to be an efficient, intuitive and exploratory methodology to describe natural disturbance boundaries. These disturbances form complex boundaries that cannot be adequately described using one-dimensional transects because of spatial heterogeneity of tree mortality and skipping of trees (Kent et al. 1997). Furthermore, it is impossible to determine with one dimensional transects if sampling is indeed perpendicular to the disturbance boundary. On the contrary, most transects in this study could not have been perfectly perpendicular because of the boundary zone spatial complexity; the inner and outer boundaries were not parallel. Other approaches that have been used elsewhere at higher spatial scales (e.g., remotely sensed data) include fuzzy set theory (Jordan 2002), probability mapping, adapted neural networks, and ordination (see review by Kent et al. 1997). These types of analysis are not suited to field collected data because of the large sample sizes needed. With field data, edge detector algorithms such as wombling (Fortin 1994) and moving split-window (Johnston et al. 1992) have been suggested techniques, though these are optimally used for detection of unknown boundaries (Fortin 1994). In situations where the presence of a boundary is not in doubt, such as those that occur in natural disturbances, but the nature and description of that boundary is unknown, constrained clustering appears to be the most efficient and intuitive.

To describe the boundaries objectively, both minimum and maximum boundary width values were calculated (MinBZ and MaxBZ respectively). While neither width calculation is more correct than the other, there are different interpretations of each. If MinBZ widths are used, then a linear representation of the boundary should be more convoluted to capture the variability. For example, in Figure 2.5C, the minimum distance was relatively small (19.5m), but there is much greater sinuosity. Furthermore, the MinBZ widths miss some of the boundary complexity. In Figure 2.5D, the MaxBZ includes spatial heterogeneity within the boundary zone

while the MinBZ shifts the mosaic structure into the disturbance itself. For applications where boundary complexity and boundary zone heterogeneity are to be considered, MaxBZ widths are a more appropriate measure (compare MinBZ and MaxBZ in Figure 2.5A). Ultimately, since forest cover polygons are, by definition, homogeneous areas of the landscape, it is more reasonable to include the variation within the boundary zone. Since this study is primarily interested in determining the size of a region of high heterogeneity, the numbers obtained from the maximum estimated widths are emphasized.

Boundary zone width ranged from 0m to 120m indicating that ND boundaries occur along a continuum of soft to hard. Overall, the boundary zones had high spatial heterogeneity of tree mortality and are equally or more heterogeneous than either the core areas of these disturbances or outside them. Boundary zones of this size (~50m) comprise ~22% of the area of the disturbance in a hypothetical circular 85 ha disturbed area (Figure 2.10). However, since no disturbance will be a perfect circle, the perimeter of a natural disturbance will be longer, creating an even larger boundary zone.

Sinuosity and heterogeneity varied with spatial resolution. Sinuosity was up to 2.5 times higher at the 5m X 5m resolution as compared to the 20m X 20m resolution. This demonstrates the spatial tension between resolution and the apparent straightness of a boundary. Thus, to say that a boundary is sinuous without reference to the scale of analysis is meaningless (Wiens 1989). Heterogeneity, as measured by the variance of plots in each zone, is spatial diversity. As expected, the MaxBZ widths showed a generally higher level of variability in the boundary zones than the MinBZ widths. This confirms that the difference between these two measures of boundary width is simply a reallocation of variability into or out of the boundary zone. Focusing on the MaxBZ values, MPB showed high variance in the boundary zone and inside the disturbance, whereas fires appeared to have most of the variability in the boundary zone. This pattern of high variability in the boundaries is not unexpected, and many people have suggested that natural boundaries are more variable than human induced boundaries (Krummel et al. 1987; Forman 1995; Foster et al. 1998). The quantification of this variability may be an important step in the analysis of natural boundaries.

As with all sampling based studies, and especially for spatially explicit studies, it is never possible to know what patterns occur immediately adjacent to the sampled plots. For instance, in Figure 2.5C, there is a large low severity cluster in the bottom right corner that could make up

another section of forest that is unaffected by the disturbance. Rather than abandon a spatially explicit methodology to avoid this problem, the use of minimum and maximum estimates reduces its impact. Averaged across all sites, the MinBZ width at the 5m sampling unit resolution was 15m for both MPB and fires. This is less than the width of any of the sampling transects; so unknown adjacent sites would likely not reduce these numbers. Furthermore, since sampling transect orientation was purposely placed approximately perpendicular to the disturbance boundary, the calculated boundary widths of both MaxBZ and MinBZ were likely minimum estimates.

In this study, the sample size at the 20m X 20m resolution was less than ideal. The patterns were consistent, however, with those detected at the two finer resolutions. Clearly, more of the fine scale heterogeneity is captured at the finer scales and there is higher sinuosity. I propose that there are sufficient samples at the coarse resolution due to the context of the two finer scales. In isolation, transects of this size with only a 20m resolution likely would not be sufficiently robust to make strong conclusions. The results at the two finer scales are robust, allowing for analysis and interpretation at 20m.

Often, natural disturbance studies examine only one type of disturbance (Cissel et al. 1999; Bergeron et al. 1999b) and rarely have there been direct comparisons between disturbance types in a single sampling study (though see Foster et al. (1998)). In addition, studies examining the natural range of variation for the purposes of management tend to look at only fires or more recently an insect outbreak (Andison & Cumming 2001). Here, an identical and simple sampling design allowed for direct comparison of spatial patterns at the boundaries of these disturbance types. Boundaries were generally steeper in fires than in MPB, but the width of these boundaries did not differ substantially. These results demonstrate that both types of natural disturbance produce a range from hard to soft boundaries. While the processes underlying fires and MPB are different, boundary widths were comparable. This may be due to the inherent spread behaviour of these natural processes. Alternatively, both fires and MPB may be responding to similar topographic features or previous disturbance signatures. These results also showed that peak severity (measured as tree mortality) of the fires was higher than MPB at all sampling unit resolutions (though with a smaller difference at 5m resolution). Clearly, these peak severity levels are determined by the nature of the sampled plots. All disturbances that could be located were sampled. These inevitably tended to be the more severe disturbance events. These

comparisons do not include lowest severity fires (of which there are few in the study area) and outbreaks. In addition, while it appears that the fires did not reach 100% severity, all fires had no living trees remaining in the core clusters. The cause of every tree death was determined as accurately as possible. Numbers below 100% therefore represent pre-fire tree mortality.

The functional differences of different boundary types, including soft and hard boundaries, has been minimally explored (Forman 1995; Fagan et al. 1999). Those that exist suggest that there are ecological differences between these two extremes of boundary diffuseness (Ratti & Reese 1988). Due to the changing function of this spatial complexity, simplifying forest disturbance boundaries of this magnitude to linear features is probably inconsistent with management objectives with respect to ENFD and certain measures of biodiversity. As the functioning of different types of boundaries is further explored, the need for a greater understanding in this area of research may become clear. The present study does not examine functional differences between these boundary types, though it provides evidence that natural disturbance boundaries are often not linear features when examined in natural disturbances of 6 to 171 ha. Implementation of this range of historical variability in managed landscapes may be important for multiple aspects of the local ecology.

Boundaries are tension zones between plant communities; they are filters allowing some things to pass through and blocking others; they are spatially complex in one and two dimensions; they are highly heterogeneous ecosystems and are ubiquitous on all landscapes; and they are a challenge for forest management and ecologists. This chapter is a preliminary demonstration that simplification of natural disturbance boundaries in forested landscapes to linear features may cause a loss of spatial complexity on the landscape. Eliminating these areas of structural diversity from the landscape through traditional forest harvesting will likely alter stand dynamics as well as landscape patterns. With operational polygons in forest management in North America between from less than 40ha to 200ha (though sometimes greater), it is difficult to ignore boundary zones that could comprise from 14% to over 30% of the polygon area.

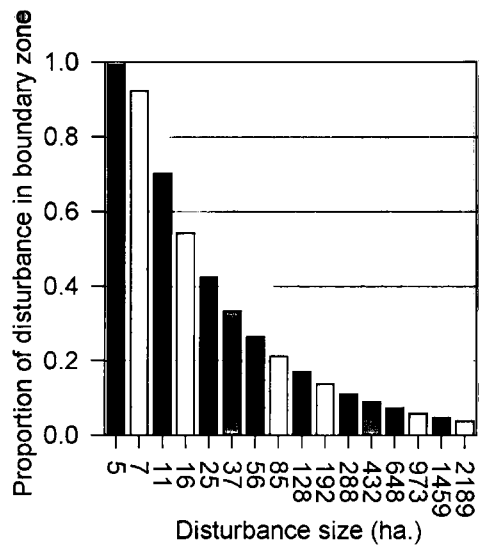


Figure 2.10. Proportion of the total disturbance area in a hypothetical circular disturbance that is contained within a 50m wide boundary. Calculations were made based on 50% of the boundary zone being included within the stated disturbance size.

Chapter 3 Understanding Natural Disturbance Boundary Formation Using Spatial Data and Path Analysis

3.1 Introduction

Natural disturbance boundaries are landscape features with high spatial variability (Wiens et al. 1985; Gosz 1991) and potentially high impacts on ecological functions (Forman 1995), yet little is known about the factors that influence their formation. For instance, do insect outbreaks stop because the insects dispersed as far as possible given the dispersal capabilities in a given period? Do fires stop due to weather events alone, or does the nature of the landscape and forest stand contribute also? Spatial variation at disturbance boundaries can be used to aid in understanding the process of boundary formation. Only in the past two decades has spatial data analysis become an available tool (Turner & Bratton 1987; Legendre & Fortin 1989; Turner 1989; Fortin & Drapeau 1995) and the spatial analysis of boundary formation a possibility. The factors influencing the cessation of a disturbance, and the creation of this heterogeneity, are the most poorly understood aspect of the disturbance event trio: disturbance initiation, propagation/dispersal, and cessation.

Two very influential natural disturbances of the Pacific Northwest of North America are wildfires (fires) and mountain pine beetle (MPB) (Agee 1993; Samman & Logan 2000). While very different, these two disturbance types share some common features. For instance, they each initiate in a localized region (though MPB may have a more diffuse initiation) and spread outwards in space (and time). This spatial similarity suggests that the influence of space on boundary creation may be important and can be used to help understand the factors that created the boundary. The precise nature of their similarities and differences is best understood by examining both within a single study.

The factors that may influence the cessation of a wildfire or MPB outbreak are particular to their biology and mechanics. MPB (*Dendroctonus ponderosae* Hopk. (Col.: Scolytidae)), is a bark beetle that kills trees upon a successful attack (Safranyik et al. 1999). The factors thought to influence the MPB outbreak at the stand scale are beetle dispersal limitation, suitable host (suitable size—often >20 cm DBH—and species—lodgepole pine), stand density, physical

environment (aspect, slope) and weather events (Stuart 1984; Samman & Logan 2000). Of these, the non-transient variables are suitable host (lodgepole pine of suitable size), density of host (thinning is thought to reduce the flight distance of the beetle), and physical factors of the landscape (aspect) (Samman & Logan 2000). Wildfires, on the other hand, are influenced by fuel load, topography and weather (including wind) (Whelan 1995). Fuel load is a function of many characteristics including species of tree, fine fuels, downed wood, and presence of ladder fuels. Topography affects local climate and its primary influence in mountainous terrain is that uphill direction acts similarly to wind direction in flatter ecosystems (DeBano et al. 1998). Fire boundaries in many areas can also be influenced by fire suppression efforts in a manner similar to a dramatic change in weather. Fires have a complex interaction with factors acting at different scales, being influenced by large scale winds that drive fire through all types of forests and by small-scale influences such as fine fuels. Some of the similarities between these two disturbances may lie in the spatial patterns.

Examining spatial relationships has two goals. First, the spatial pattern of a phenomenon may be the primary interest (Asselin et al. 2001). This is the case when one is interested in determining the relevant scales for analysis of an ecological phenomenon, examining whether there is spatial autocorrelation in the data, or simply describing the spatial pattern. Second, and perhaps more powerfully, one may be interested in determining whether there is spatial structure in the data that can act as a surrogate for other unmeasured or unmeasurable components of the system (Leduc et al. 1992). For instance, knowing that there is no spatial autocorrelation in a given data set allows a researcher to fulfill a major assumption in frequentist analyses (based on the Gaussian distribution) of independence of data points (Fortin & Gurevitch 1993). Furthermore, most ecological processes and landscape features are spatially autocorrelated (e.g., dispersal, slope angle, fire propagation). Detecting a spatial pattern in data implies the presence of a spatial process that was not measured. Thus, space can act as a surrogate for other variables that were not included in the study (Fortin & Payette 2002), though it cannot be used to precisely infer the cause of this spatial pattern. However, useful inferences can be made when space is found to not influence the data; in this case, other spatially defined, but unmeasured, variables would not be necessary to account for the data.

Path analysis via structural equation modeling is a statistical analysis technique used primarily to test the fit of data to *a priori* causal hypotheses about the functioning of a system

(Wright 1921; Schemske & Horvitz 1988; Shipley 2000). Like all *a priori* hypothesis testing techniques, it requires thoughtful generation of plausible hypotheses based on existing knowledge and scientific understanding. Unique to path analysis (and other Structural Equation Modeling techniques), is the positing of direct and indirect effects as well as asymmetric—or causal—effects (Bollen 1989; Wootton 1994). Indeed, while path analysis allows for causal inference, it does not prove a causal relationship and is not a panacea for non-experimental studies (Petratis et al. 1996). Rather, wherever possible, experimentation is generally preferable to deduce causal mechanisms and, ideally, path analysis should be used in conjunction with experimentation (Wootton 1994). However, by far the majority of ecological questions are not conducive to traditional experimental testing. For instance, questions about the effects of wildfire on a forested landscape at any scale can only be estimated by the use of prescribed burning because of the different environmental and weather conditions that occur during prescribed burns and wildfires. Furthermore, even if wildfire conditions could be recreated within a prescribed burn, the almost universal impossibility to do satisfactory replication precludes any statistical inference. A similar set of criticisms can be applied to studies that manipulate only one or few factors. The problem of rebuilding individual component processes into a whole picture is well known because of the complexity of multiple factors acting in conjunction (Peters 1991). While path analysis does not fully resolve these issues, it has many of the benefits of observational studies, allowing for all the complex interactions of nature to occur, yet with some of the benefits of manipulative studies. Essentially, path analysis profits from controlling variables in the same way as an experimental study, but uses statistical controls rather than physical controls. Examples of successful application of path analysis in non-experimental ecological situations are numerous (Mitchell 1992; Lundquist 2000; Shipley & Lechowicz 2000; de Blois et al. 2001), and include problems such as separating biotic and abiotic influences of species richness in coastal wetlands (Grace & Pugsek 1998).

The primary objectives of this chapter are to translate existing knowledge of wildfire and MPB processes into *a priori* hypotheses about the creation of disturbance boundaries and then to test these hypotheses about the creation of wildfire and MPB boundaries. I use *a priori* multiple hypothesis testing using causal path hypotheses with spatial variables explicitly modeled and an information-theoretic approach (Burnham & Anderson 1998). In particular, I will test spatially explicit hypotheses using factors that asymmetrically influence (“cause”) wildfire and MPB

boundaries to occur. These hypotheses are represented as graphical path models (Figure 3.1). Since this analysis occurs only at a single scale, this is not an attempt to actually predict where and why a fire or MPB outbreak will stop during an event or outbreak. Instead, it is an attempt to understand the relative contributions of measurable stand variables and unmeasurable transient variables, using space as a surrogate, to the cessation of these natural disturbances in mountain forest landscapes.

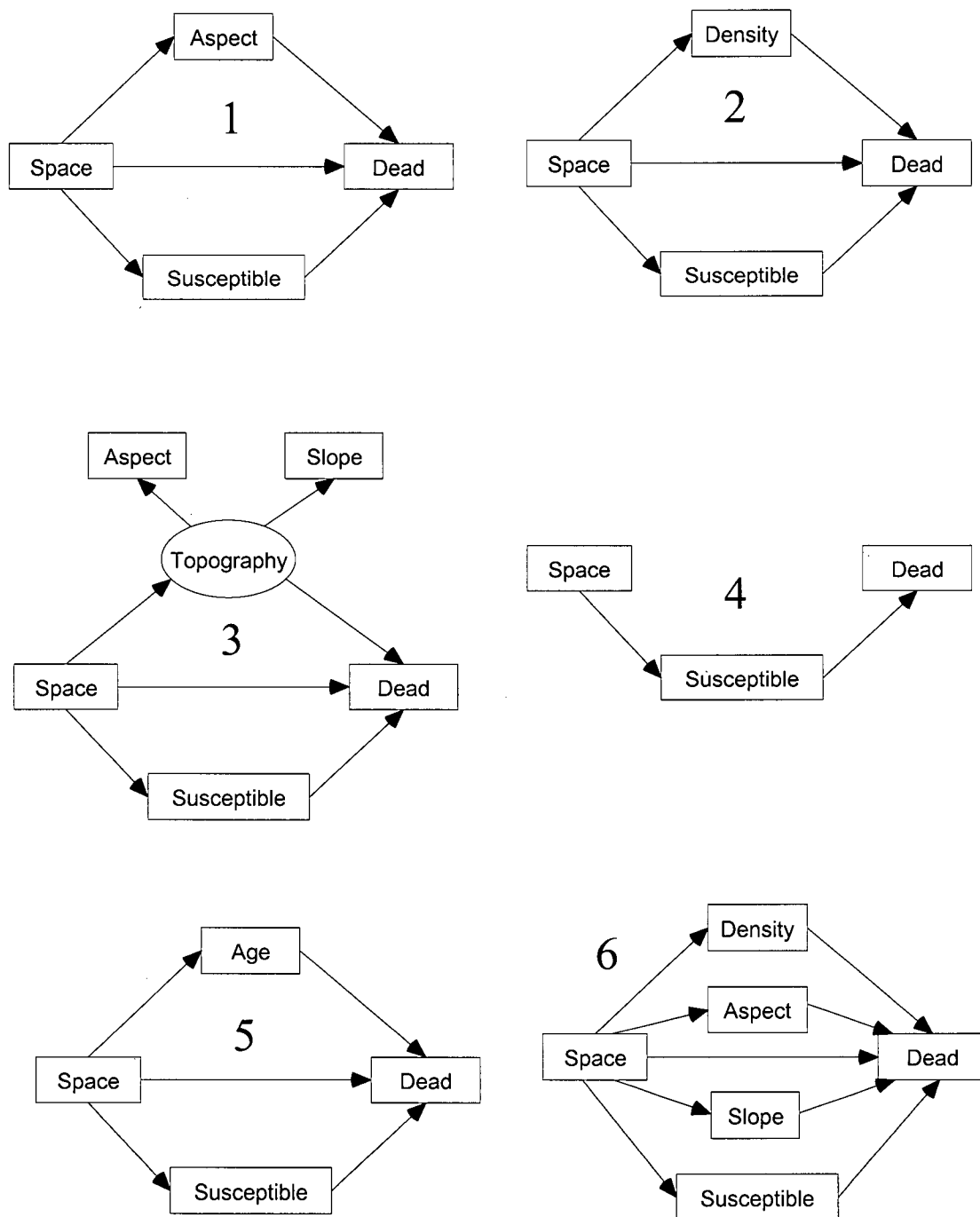


Figure 3.1. Hypothesized path models. All error terms are left out of the diagrams for clarity. Every endogenous (has a hypothesized factor affecting it) variable has an error term representing all unmeasured factors that influence the variable. Since there is only one exogenous factor (space), there are no unresolved covariances.

3.2 Methods

3.2.1 Study Area and Study Design

Research was conducted in the Arrow Lakes and Kootenay Forest Districts, in south central BC, Canada within three biogeoclimatic zones (ICHmw2, ESSFwc1, and ESSFwc4 (Meidinger & Pojar 1991)). All MPB sites were dominated by lodgepole pine (*Pinus contorta*) and fire sites were dominated by lodgepole pine, subalpine fir (*Abies lasiocarpa*), white X Engelmann spruce hybrids (*Picea engelmannii* X *glauca*), or Douglas-fir (*Pseudotsuga menziesii*). These zones are characterized by stand replacing fire disturbance regimes, ranging from 150 years to 400 years (NDT 1 and 2, rare or infrequent stand initiating events) (Ministry of Forests & Ministry of Environment 1995).

In the summer of 2001, 18 two-dimensional sampling transects were used of which seven were from five different fires (sites 12 and 20, and 17 and 21 were from the same fires, however, the transects were separated by at least 1 km from each other). All disturbances occurred between 1993 and 1997. Fires sites were lightning caused, had extensive areas that were not salvaged, were physically capable of being sampled (i.e., no slopes $>50^\circ$), occurred at elevations between 1400m and 1900m, and were in the province's fire database (Protection Branch 2001). All fires had active fire suppression efforts, however, site selection within each fire was constrained to sites where there was no or minimal evidence of local suppression efforts (e.g., no Pulaski fire guard lines, red retardant embedded in down wood, evidence of trees cut during the fire). Fire boundaries examined in this study were horizontal across the mountain slope along the side flanks of the fire event so all inferences to aspect and slope are sideways across the slope (i.e., along the contour), rather than at the top of the slope. The eleven MPB sites had the following characteristics: mature stands (60 years $<$ tree age at DBH $<$ 150 years); canopy trees at least 20 cm, DBH; southerly aspect slopes (97° to 256°); elevation between 1150m and 1550m. MPB stands were overall of similar character due to the selective nature of the insect disturbance (mature lodgepole pine), though the secondary tree species and understory vegetation were not necessarily similar throughout. Placement of transects was random within a given disturbance boundary (see Chapter 2). Transect length was determined on a site-by-site basis to encompass both the peak severity of the disturbance event and an area outside the

mortality. Plots within each transect were contiguous and were 10m X 10m (100m²)⁹. Sites used in this study for both fire and MPB represent a full census of those that were accessible to sampling, given the sampling area and identified populations.

Sampling occurred using 2-dimensional sampling transects that ranged from 60m to 170m long and 40m to 60m wide. However, given the causal hypotheses used in this study, space was modeled as a continuous variable in only one dimension, represented by the longitudinal data (i.e., the long axis). This simplification was used for several reasons. It was decided based on the analysis of two-dimensional data reported in Chapter 2 that the longitudinal trend could be approximated using the single long axis. Furthermore, given the sample sizes at each site, the addition of the latitudinal variable increased model variance (uncertainty) and reduced degrees of freedom with very little added information.

3.2.2 Transient vs. Non-Transient Factors

For the purpose of this study, it is assumed that there are two general classes of factor affecting the cessation of a fire or a mountain pine beetle outbreak. These can be either internal to the forest system—non-transient—and are therefore estimable after the fire or outbreak has stopped; or external to the forest system—transient—and are unmeasurable after the event (Perry 1988). Non-transient factors used in this study include such factors as slope and aspect (and edaphic changes that are correlated to these), tree density, tree age, tree size and tree species. Transient factors could include edaphic features related to the moisture conditions at the time of the fire, temperature, wind, weather, parasitoid abundance, beetle source, beetle abundance, beetle movement speed and distance. These latter factors cannot be measured within the forest after the events have occurred, though most of them have a spatial component that acts at scales represented in this study (e.g., 60 to 170 m extent at 10 m resolution). For instance, wind moves from a direction for a period, then may shift to come from a different direction. Insect movement during a given dispersal event is spatially non-random; there is a source (or several sources) and the beetles move outward from this source, creating a spatially constrained pattern on the landscape. Clearly, a transect across the boundary of a disturbance event will have some a

⁹ Because variables in this chapter include those that were only collected at the 10m X 10m resolution (see Table 1.1), all analyses are only performed at this resolution.

spatial component since a boundary is defined as being a location in which tree mortality changes rapidly in space.

3.2.3 Correlation Analysis

Pearson correlations between all independent variables posited in the path models (e.g., slope, tree density etc.) and plot mortality were calculated to show the correlation patterns in these sites. These correlations were also presented to demonstrate the added information gained by using a spatial variable within a path model framework.

3.2.4 Multiple Hypothesis Path Models

A multiple hypothesis framework for data analysis requires several adjustments from standard null hypothesis modeling (Chamberlain 1890; Anderson et al. 2000; Zucchini 2000; Anderson & Burnham 2002). First, absolute measures of fit (e.g., the probability level in null hypothesis testing) are replaced with relative measures of fit, comparing the level of confidence among proposed models. Consequently, in a multiple hypothesis framework, inference is only as strong as the models being tested, however, there is no arbitrary point of demarcation (e.g., $p < 0.05$). Second, models should be generated *a priori*. This means that models should be generated prior to data collection based on pre-existing theories of the processes being studied or from preliminary studies. In this study, many areas within the Arrow Lakes were visited in the year preceding data collection. The hypotheses in this study were generated based on literature and this pilot study.

Sites were not explicitly used as replicates of one another; I allowed for different model support at each site. Since there were between 24 and 68 plots at each site, there was sufficient plot level replication to allow for a separate path analysis at each site. Rather than suggest that the same causal hypothesis applies at all sites, results were summarized to show proportion of the sites at which the factors proposed within each model influence boundary creation.

The path models used are shown in Figure 3.1. The logic behind each of these models follows. All models include a variable representing spatial position along the transect since it is impossible that mortality will not have a spatial trend. The uncertainty is how strong an effect it has and whether it will be indirect acting through other factors or direct (not be accounted for in the other modeled variables). Space is modeled throughout as directly affecting mortality and

indirectly affecting mortality through the other variables. Only in model 4 is space limited to taking an indirect effect.

Four other factors are included in the models. The first is the presence and abundance of susceptible trees to the given disturbance agent (Susceptible). All trees greater than 10 cm diameter at breast height were measured in all plots. For MPB, this variable is modeled as basal area of lodgepole pine (BA) per plot. No effort was made to isolate only trees of a given size (e.g., over 20 cm DBH) as the nature of BA is that larger trees influence the metric as a function of the square of their diameter. Thus, a 30 cm DBH tree influences the BA quantity 4 times that of a 15 cm tree. Furthermore, there is no absolute size cutoff for mountain pine beetle; in some sites, only trees over 20 cm DBH are affected, while at others, trees over 15 cm DBH are affected (Safranyik et al. 1999). For fires, susceptible trees are all trees species whose bark is not thick enough to offer protection and that do not withstand surface fires (Susceptible). Thus, non-susceptible trees are ponderosa pine (Pp, *Pinus ponderosa*), western larch (Lw, *Larix occidentalis*), or Douglas-fir (Fd, *Pseudotsuga menziesii*), and susceptible trees are lodgepole pine (Pl, *Pinus contorta*), western redcedar (Cw, *Thuja plicata*), western hemlock (Hw, *Tsuga heterophylla*), subalpine fir (Bl, *Abies lasiocarpa*), and hybrid spruce (Sx, *Picea glauca* X *engelmannii*) (Crane & Fischer 1986; Agee 1993). Hardwood trees were virtually absent from these sites. Again, no distinction in diameter was made; since larger trees disproportionately influence basal area, smaller trees of these less susceptible species would have little impact.

The second factor is age of the plot as estimated by a single tree core at breast height to pith of a canopy tree in each plot. Since age calculated at breast height is a highly variable estimate of age (not very accurate), transect level variation will be very high. Thus, modeling age using this strategy is primarily sensitive to large age differences across the transects. Age is predicted to be a factor in MPB stands if the stand has a distinct shift in age, from an older, mature stand, to a younger stand. This type of influence would represent the ecological footprint of a past disturbance event, such as a fire, creating the landscape structure that current disturbances may follow.

The third factor is stand density. One strategy for managing MPB stands is to thin trees to a given stems per hectare because this is thought to reduce the impact of MPB attacks (Safranyik et al. 1999).

The final factor is the physical environment. This was modeled in two ways; first, as aspect (Aspect) rescaled with south at zero and the absolute value of the degrees east or west. All sites occurred on southerly facing aspects; this rescaling weights shifts to east or west equally to examine the effect of a shift away from due south. Second, topography was modeled as a latent variable that influences slope (Slope) and aspect. Each of these factors is modeled as a direct effect on mortality, one at a time, and simultaneously (model 6).

Many models built with the interactions of these five variables were eliminated *a priori*, including the possibility of environmental variables directly affecting tree abundance (BA susceptible). Models were eliminated *a priori* because of limited sample sizes and the desire to limit the number of models to those most plausible.

All models were tested for absolute fit as well as relative support (see below) by comparing all models at each site. Root mean squared error of approximation (RMSEA) and comparative fit index (CFI) were used as goodness-of-fit statistics (Bentler 1990; Browne & Cudeck 1993). Models that have either RMSEA<0.06 or CFI>0.95 are considered to have a good fit, in an absolute scale. Models were first tested for absolute fit then compared to one another because if no model was considered “good fitting”, then relative comparisons would be less meaningful. Model comparisons were done using modified Akaike’s Information Criterion for small samples (AIC_c), as defined for use with structural hypotheses (Akaike 1987; Burnham & Anderson 1998). The formula appears slightly different than the standard AIC formula as the model discrepancy is used which is calculated as the difference between the negative log likelihood of the selected model and the negative log likelihood of the saturated model. Model analysis is performed using AMOS structural equation model software (Arbuckle 1999; Byrne 2001). AIC_c is calculated external to the software as:

$$AIC_c = \chi^2 - 2 \cdot d.f. + \frac{2K(K+1)}{n-K-1}$$

where χ^2 is the chi-squared discrepancy, d.f. is the degrees of freedom of the model (total number of parameters in the model minus the total number of estimated parameters), K is the number of parameters and n is the sample size. This calculation is used throughout this paper for model comparison (AIC_c was also calculated from the formula included in AMOS software, which replaces the “-2*d.f.” term with “+ 2 * # estimated parameters”. This is not the equation used by Akaike (1987); however, the differences between these two calculations of AIC do not

significantly change interpretation of results. In general, the “best” model was the same using the two methods of calculating AIC_c . However, the AIC_c used in AMOS removed model selection uncertainty since the second best models were never within $\Delta_i=3.8$. Results are presented and discussed using Akaike’s original calculation).

Akaike weights (Δ_i) and normalized Akaike weights are presented (w_i). In general, where $\Delta_i < 3.8$, the models can be considered to have equivalent support, where $3.84 < \Delta_i < 7$ to 10, the models may have support, however, it is unlikely. Below these values, it is highly improbable, given the data, that the model describes the data. To account for model selection uncertainty (i.e., where several models have similar probabilities of being the “best” candidate model), parameter estimates presented here are averages from all models in which the parameter occur, relativized to level of support for each model (Burnham & Anderson 1998).

All data presented from path analyses use normalized variables (mean=0, variance=1) and represent correlation coefficients (“r”) between the variables. All analyses are tested for multivariate normality prior to analysis (Mardia 1970; Arbuckle 1999). Most sites fulfilled strict multivariate normality for each path model (Path model 1 for 14/18 sites; Path model 2 for 12/18; Path model 3 for 11/14; Path model 4 for 15/18; Path model 5 was not estimable because of missing values in age; Path model 6 for 11/18). The results from some sites for path model 3 were not valid because of negative variances. These particular sites were removed from the analysis and they are represented as N/A in tables (and resulted in a sample size of 14 for model 3). Departures from normality were usually from critical values < 4 . Furthermore, path models 1, 2, 4 and 5 had sample sizes well over 10 times the model degrees of freedom (many $> 40 \times$ d.f.). Path models 3 and 6 had sample sizes over 5 times the model degrees of freedom. These results of the tests for multivariate normality suggest that the departures should not strongly influence results (Hoogland & Boomsma 1998). Therefore, no transformations of variables from sites that were not normally distributed were performed.

In all analyses, the dependent variable representing mortality is calculated as basal area of the dead trees per plot (Dead), standardized for the total basal area of the plot (BA killed/[BA killed + BA alive]). For simplicity, representation of this variable in figures and text is just “dead” or “mortality”. Results will be discussed using the explicit term “BA dead”. Because the influence of space is likely to be acting at different scales (Chapter 2), the non-standardized coefficients will have little real meaning. This study was not designed to examine the effect of

scale. The use of standardized coefficients has strengths—namely, that results can be compared between studies—and weaknesses—standardized coefficients do not show the slope of the relationship (Grace & Pugsek 1998; Shipley 2000). Since the slope of the relationship was not the focus of this study, the standardized coefficients were used.

Within the path model framework, regression coefficients can be examined to provide a basis for understanding the relationships within the models. Strictly speaking, only those path models that have strongest support should be analyzed for their regression coefficients. Here, I present statistically significant coefficients from all models, but these numbers should not be interpreted as robust in cases where the path models have little support.

3.3 Results

3.3.1 Correlation Analysis

Initial Pearson correlation matrix shows that there was a significant relationship between space and mortality in all sites (Table 3.1). Furthermore, 8 out of 11 MPB sites showed a significant relationship between stand density and mortality and three out of eleven MPB sites showed a significant relationship between stand age and mortality. Three out of seven fire sites showed a significant relationship between mortality and either aspect or slope and four out of seven fire boundaries showed an effect of susceptibility on mortality. Two out of seven fire sites showed a relationship between density and mortality and one showed a relationship between age and mortality.

3.3.2 Multiple Path Hypotheses

All sites had at least one path model that demonstrated a good fit, based on either RMSEA or CFI (Table 3.2). In 16 out of 18 sites, the best model or models as chosen from AIC_c showed a good fit based on both measures of absolute fit. Of the two sites where low AIC_c did not correspond with a good fitting model (F18 and F21), Δ_5 for F21 was 5.4 indicating that it could be a good model within the AIC framework, and F18 had a very small sample size (due to the fact that it had a very hard edge). As a result, F18 had no good fitting model that was selected using AIC_c . Nonetheless, the AIC_c selected model at F18 was model 1, consistent with all other fire sites.

Path models 1 and 4 had consistently the highest level of support across the sites (Table 3.2 and Table 3.3). Fires were better described by path model 1 and MPB sites were better described by path model 4. Model 4 is the similar to model 1 but without three of the paths: a direct influence of Space on Dead, Space on Aspect and Aspect on Dead. However, of the sites where model 4 was selected, none of the paths from Aspect to Dead was significant ($p>0.1$) indicating that the added strength of this model is derived primarily from the incorporation of the direct affect of Space on Dead and of Space on Aspect.

Beyond these general results, path model 5 had support at sites M13, F12 and F21 (Tables 3.2 and 3.3 and 3.4). This model differed from model 4 in that it replaces the effect of Aspect with Age. The affect of Age on Dead was not significant in any of these models ($p>0.1$). Rather, the support for this model at these three sites is conferred by the path from Space to Age ($r=0.35$, $r=0.53$, $r=0.24$, respectively). Path model 2 had support at site M16. The path from tree Density to Dead, however, was not strong or significant ($r=-0.05$, $p>0.1$). Path model 6 had very strong relative support at site M2 (though RMSEA and CFI were not good). This strength of support derived from significant relationships between Space and Density ($r=-0.645$, $p>0.01$), Density and Dead ($r=-0.23$, $p=0.04$). A negative relationship between Density and Dead is opposite to that predicted. Neither Aspect nor Slope contributed a significant path to the model.

All relationships between basal area of susceptible trees (Susceptible) and mortality (Dead) were positive (Figure 3.2). All fires and 91% of MPB boundaries showed a significant relationship between susceptible host and mortality. Significant coefficients for MPB were very strong ranging from 0.52 to 0.92. This effect was positive at all sites, indicating that mortality increases with increasing basal area of susceptible trees.

3.3.3 Influence of Spatial Location

All sites showed a significant effect of space on mortality (Table 3.4) with coefficients ranging from 0.21 to 0.81 (Space on Dead) and indicating a strong predictive relationship between space and mortality across the boundary (Figure 3.3). All of the influence of space in fires boundaries can be attributed to its direct effect. Over 63% of MPB sites showed only an indirect effect of space on the mortality pattern. Nearly 29% of fires boundaries showed a spatial pattern in the fire susceptible trees, whereas, 73% of MPB boundaries showed a spatial pattern in the BA of susceptible host trees (Table 3.4). These coefficients ranged up to 0.78 (Figure 3.2).

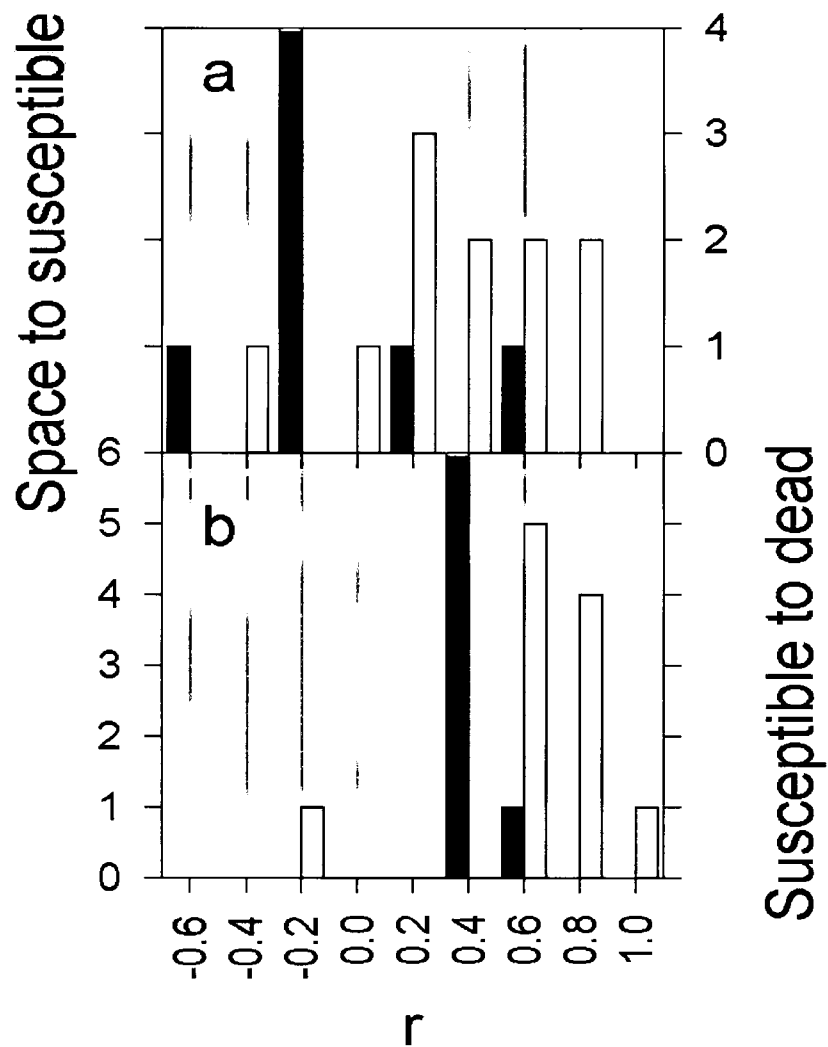


Figure 3.2. Histograms of standardized correlation coefficients of the a) effect of space on susceptible trees and b) influence of basal area of susceptible trees on mortality. X-axis represents the middle of the histogram bin ranges. Black=fire, gray=MPB.

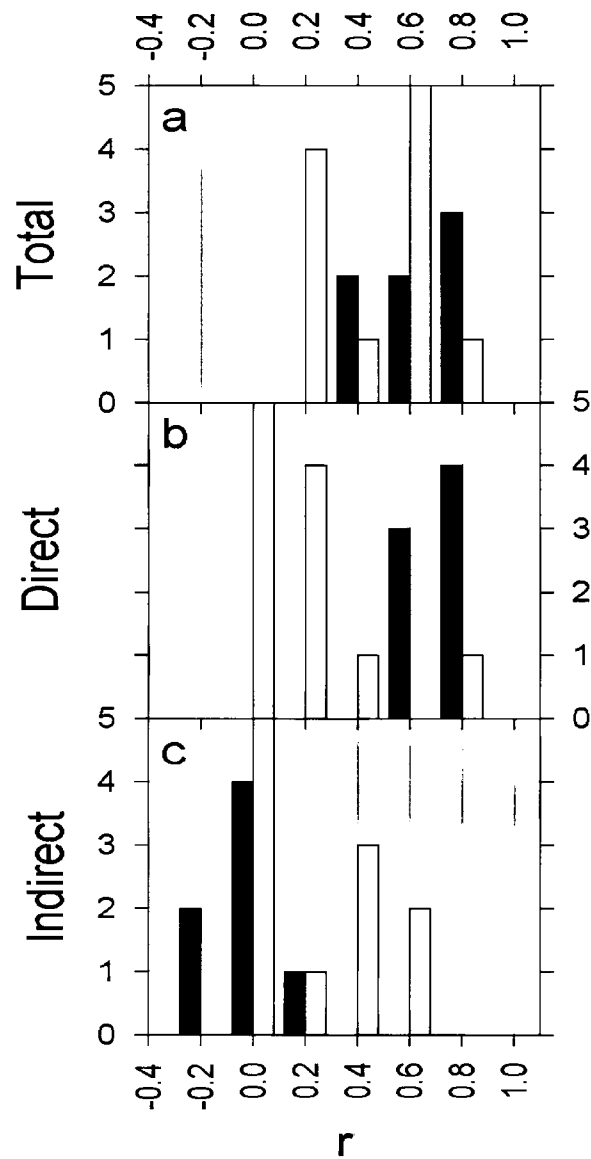


Figure 3.3. Histograms of standardized correlation coefficients of the influence of space on mortality. a) total, b) direct and c) indirect effects of space are shown. X-axis represents the middle of the histogram bin ranges. Black=fire, gray=MPB.

Table 3.1. Correlation matrix of Pearson correlations between all independent variables and BA dead (dependent variable throughout) for all sites sampled.

	Site	Space	Susceptible	Aspect	Slope	Density	Age
	M2	<i>0.54**</i>	<i>0.64**</i>	-0.29	-0.06	<i>-0.30*</i>	<i>0.68**</i>
	M3	<i>0.56**</i>	<i>0.92**</i>	<i>-0.40**</i>	<i>-0.36*</i>	<i>0.33*</i>	0.13
	M5	<i>-0.34**</i>	<i>0.87**</i>	<i>-0.24*</i>	-0.10	<i>0.42**</i>	-0.03
	M6	<i>0.30*</i>	<i>0.78**</i>	0.05	0.00	0.17	0.10
	M8	<i>0.61**</i>	<i>0.87**</i>	<i>0.47**</i>	<i>-0.29*</i>	<i>0.62**</i>	0.05
	M9	<i>0.33**</i>	<i>0.70**</i>	0.04	<i>-0.31*</i>	<i>0.26*</i>	0.12
	M10	<i>0.61**</i>	<i>0.74**</i>	<i>0.43**</i>	-0.14	<i>0.65**</i>	0.25
	M13	<i>0.71**</i>	0.16	-0.15	-0.13	-0.26	<i>-0.40**</i>
	M14	<i>0.56**</i>	<i>0.66**</i>	<i>0.53**</i>	<i>-0.47**</i>	<i>0.31*</i>	<i>0.49**</i>
	M15	<i>0.30*</i>	<i>0.57**</i>	0.04	-0.05	<i>0.32*</i>	0.06
	M16	<i>0.29*</i>	<i>0.66**</i>	0.02	<i>0.33*</i>	-0.24	0.00
	F11	<i>0.80**</i>	<i>0.47**</i>	0.07	<i>-0.50**</i>	<i>0.59**</i>	-0.08
	F12	<i>0.73**</i>	<i>0.27*</i>	<i>-0.52**</i>	<i>0.50**</i>	0.09	-0.15
	F17	<i>0.45**</i>	<i>0.37**</i>	<i>-0.31**</i>	0.00	0.20	0.11
	F18	<i>0.56**</i>	0.36	-0.37	0.16	0.04	-0.20
	F19	<i>0.62**</i>	-0.09	<i>-0.53**</i>	-0.21	-0.02	-0.03
	F20	<i>0.81**</i>	<i>0.70**</i>	-0.22	<i>-0.64**</i>	0.21	<i>0.46**</i>
	F21	<i>0.59**</i>	0.20	-0.08	-0.17	<i>0.33**</i>	0.12
Percent	MPB	100%	91%	45%	45%	73%	27%
significant	Fire	100%	57%	43%	43%	29%	14%

Table 3.2. Path model results. Numbers represent AIC_c differences (Δ_i). Bold= $\Delta_i < 3.84$, underline=CFI>0.95, *=RMSEA<0.06. # times best model is where $\Delta_i = 0.0$. # times <3.84 is where the path model is statistically indistinguishable ($P(\chi^2|3.84=0.05)$). # good models is where both Δ_i and either RMSEA or CFI were considered the path model good.

Site#		Path Model #							
			1	2	3	4	5	6	
	Min	d.f.	1	1	7	1	1	6	# good
N	AIC _c	# Param.	9	9	14	5	13	15	models
M2	44	0.5	3.1*	8.5	N/A	27.7	11.1	0.0	1
M3	40	0.2	6.7	17.4	N/A	0.0*	17.5	27.3	1
M5	68	-1.0	2.2*	23.5	N/A	0.0*	5.9*	18.4	2
M6	48	2.7	0.0*	6.7	N/A	1.3	8.0	5.0	1
M8	56	-0.8	3.1*	24.3	3.9*	0.0*	7.4*	26.5	2
M9	60	1.4	3.4	20.7	4.7	0.0	6.5	11.0	2
M10	52	-0.4	3.0*	27.7	3.9*	0.0*	10.3	20.8	2
M13	48	8.9	1.4	48.5	N/A	24.8	0.0*	53.9	1
M14	60	2.5	0.0*	30.6	2.5	2.1	8.9	16.1	3
M15	56	-0.8	2.9*	22.2	N/A	0.0*	7.9*	9.1	2
M16	56	1.9	1.4*	0.0*	N/A	1.1	6.8	24.3	2
# times best model			2	1	0	6	1	1	
# times within 3.84			10	1	1	9	1	1	
F11	48	2.9	0.0*	15.0	N/A	52.7	8.6	17.5	1
F12	64	4.6	0.0	68.1	1.1	57.0	1.1*	69.7	3
F17	60	3.9	0.0	16.8	N/A	19.8	7.2	50.5	1
F18	24	13.9	0.0	11.2	14.3	3.8	21.6	43.3	0
F19	40	4.0	0.0*	34.9	N/A	25.2	9.8	35.8	1
F20	44	3.5	0.0*	31.2	1.1*	25.1	14.9	21.3	2
F21	52	4.8	0.0	35.7	N/A	21.7	5.4	30.2	1
# times best model			7	0	0	0	0	0	
# times < 3.84			7	0	2	0	1	0	

Table 3.3. Akaike weights, $w_i = \frac{\exp(-\Delta_i/2)}{\sum_{r=1}^R \exp(-\Delta_r/2)}$. These can be interpreted approximately as the

probability that a model is the best model (Burnham & Anderson 2001). Weights >0.05 are indicated by bold typeface.

Site	Path Model #					
	1	2	3	4	5	6
M2	0.172	0.012	0.001	0.000	0.003	0.812
M3	0.033	0.000	0.000	0.966	0.000	0.000
M5	0.242	0.000	0.000	0.720	0.037	0.000
M6	0.599	0.021	0.000	0.319	0.011	0.049
M8	0.153	0.000	0.106	0.724	0.017	0.000
M9	0.141	0.000	0.072	0.755	0.029	0.003
M10	0.161	0.000	0.106	0.729	0.004	0.000
M13	0.332	0.000	0.000	0.000	0.668	0.000
M14	0.606	0.000	0.170	0.217	0.007	0.000
M15	0.187	0.000	0.000	0.790	0.015	0.008
M16	0.233	0.477	0.000	0.274	0.016	0.000
F11	0.986	0.001	0.000	0.000	0.013	0.000
F12	0.464	0.000	0.263	0.000	0.273	0.000
F17	0.974	0.000	0.000	0.000	0.026	0.000
F18	0.865	0.003	0.001	0.131	0.000	0.000
F19	0.993	0.000	0.000	0.000	0.007	0.000
F20	0.639	0.000	0.361	0.000	0.000	0.000
F21	0.936	0.000	0.000	0.000	0.064	0.000

Table 3.4. Proportion of sites for which each relationship has a significant path coefficient ($p < 0.05$). This is equivalent to a significant regression coefficient in a multiple regression. Sites with significant values for density (F11, M14) and age (M2, F18) did not have support for the path models 2 and 5, respectively.

Relationship	Based on path		
	model #	Fire	MPB
SpaceTotal on Dead	1	100%	100%
SpaceDirect on Dead	1	100%	36%
SpaceIndirect on Dead	1	0%	64%
Space on Susceptible	1	29%	73%
Susceptible on Dead	1	100%	91%
Aspect on Dead	1	14%	0%
Space on Aspect	1	43%	64%
Density on Dead	2	14%	9%
Age on Dead	5	14%	9%

3.4 Discussion

This study suggests that both fires and MPB boundaries are fundamentally similar by being influenced directly (and positively) by the basal area of susceptible trees. On the other hand, space (as measured by the linear distance across the boundary) appears to act directly on fire boundaries at all sites, but indirectly on MPB boundaries (7/11 of sites). Approximately 4/11 of MPB sites have a direct effect of space on the pattern of mortality. This difference between direct and indirect effects of space suggests that modeling MPB dispersal (inherently spatial) as a means of understanding where they will stop will only be relevant in 4/11 of the sites in this area (see below). Furthermore, path models that included Age, Density, Aspect and Slope had little support from the data. Where there was support for models that included these variables, the paths conferring model support were not between these variables and mortality, except in one case between density and mortality. Thus, these factors have little influence on the creation of the boundaries in these study sites.

AIC_c selects the best fitting model and gives advantages to parsimonious models, penalizing for the number of estimated parameters that are in the model. Results from this study indicate that there were often more than one model supported by the data. For example, both models 1 and 5 are “good” at site F12. Since none of the paths between environment and dead, age and dead, or density and dead is significant (except for site M2), then the similar support for each of these different models has no effect on mortality. Some of the model selection uncertainty (similar AIC_c values) is derived from strong paths between Space and factors such as Density, Age, and Environment. Since the goal of this chapter is to determine the relative influences of factors on mortality, these isolated significant relationships are of little importance. Thus, models 1 and 4, which consistently have high support, appear to be largely responsible for the data, given the models that are being analyzed.

3.4.1 Influence of Spatial Location

That both disturbance type boundaries show a significant effect of space is not surprising. Clearly, a spatial effect will be found given that a disturbance boundary is defined as an area with a spatial change in mortality. What is not apparent from a cursory examination of a

disturbance boundary is whether space is a direct influence on the boundary or indirect. The inference of these two alternatives is very different. An indirect effect of space indicates that while there is indeed a spatial component to the data, something else is the proximate cause of the pattern. In this case, the MPB boundaries have a spatially defined pattern of host (73% of the sites) that appears to drive the boundary mortality. Furthermore, when space is an explicit variable within the models, potentially confounding factors can be isolated. For instance, if tree density varies across the plots and tree mortality also varies across the plots in the same direction (as is the case in many sites), a study without space explicitly modeled cannot further resolve the causal structure of these patterns.

A significant effect of space, in isolation, is often not the object of interest in a study. Space acts as a surrogate for all spatially autocorrelated factors that were not or could not be measured (e.g., transient factors). In this case, the significant direct effect of space on wildfires indicates that the fires were also influenced by spatial factors, in addition to non-transient variables measured here. While it is impossible to specify these potential effects, space most likely reflects the influence of weather or local moisture and edaphic conditions during the fire event, since these are likely the primary influences on a fire's propagation. Clearly, other influences such as the pattern of fine fuels on the ground, tree canopy architecture, presence of ladder fuels, the onset of rain, or even the direct or indirect influence of fire suppression efforts could also contribute to this significant direct spatial effect. That there is no significant indirect spatial effect at any fire site suggests that it is not the spatial pattern of susceptible trees (Pl, Cw, Hw, Bl, Sx) influencing the mortality pattern; rather, it is the presence or absence of susceptible trees that has influenced the boundary, regardless of their distribution along the boundary transect.

The difference between a direct and an indirect effect of space for MPB sites likely relates to the difference between transient factors and non-transient factors. The strong indirect influence of space in MPB sites indicates that not only is the mortality pattern a function of the susceptible trees, but also of where the susceptible trees are across the boundary. This suggests that the outbreak at seven of 11 sites was host limited and that the host distribution was spatially arranged across the boundary. This may suggest that if there had been more host abundance, the outbreak would have continued further. The four of eleven sites that had only a direct effect of space indicates these outbreaks were not host limited. In these cases, transient factors may have

been influential; the most likely spatial factor affecting mortality is MPB dispersal. Indeed, this result indicates that more living host trees (PI) occurred beyond the current boundary. The implications for population biology interpretations of this pattern are that modeling MPB dispersal to understand the cessation of the outbreak will only be relevant in a proportion of the cases (approximately 1/3), if this ratio is similar in other areas. The ratio will probably vary by site and region, but this type of inference is generally not available using standard methods of data analysis.

3.4.2 Non-Transient Factors

Plot tree density, tree age, aspect, and slope have all been posited to influence natural disturbances (Samman & Logan 2000). In an initial examination of the correlation matrix of these variables, one would conclude that these are related to boundary mortality. With *a priori* model testing, space is deduced to be the common cause of each of these variables: density and mortality, age and mortality, aspect and mortality, and slope and mortality. Some sites showed support for the path models that included these variables. The support for these models, however, was not due to the direct influence of these variables on pattern of mortality. Rather, as can be seen in the path diagrams, there are paths from space to these variables that were significant. While it is not possible to attribute a high goodness-of-fit to any particular path in a full model, the relationships between these variables and mortality were not significant at any site. This demonstrates that these paths are not responsible for the added fit of the models and that there is little support for a relationship between these variables and mortality.

Path modeling has been used elsewhere to untangle causal relationships in situations where experimental manipulations were not possible (Grace & Pugsek 1998; Lundquist 2000; Shipley & Lechowicz 2000; de Blois et al. 2001). The knowledge gained here over a simple correlation analysis (noting that the one presented here is not meant as a comparison of a robust analysis, rather, simply a baseline set of correlations with which to compare path model results) can be substantial. The different interpretations for the ecology responsible for the cessation of a natural disturbance, whether the effects are direct or indirect, are important due to the inferential differences. Many imaginable hypotheses were not tested in this study, thus the inferences from the “best” hypotheses presented here are only the best given the available models. Since there was absolute good fit for these models and the relative support was used to select the best

models, I can simultaneously reject several mechanisms (e.g., aspect, density) for boundary creation and provide support for a small set of causal models. Even in experimental studies, however, the best that can be done is the rejection of hypotheses; hypothesis cannot be proven, they can only gain support (Popper 1979). As demonstrated here, path models provide a much better understanding of natural systems that cannot be manipulated than regression type studies. Moreover, when used in conjunction with multiple hypotheses, the validity of the path model can be examined on a relative scale. The successful models can then be taken to a new set of sites and tested there. Furthermore, the influence of space can be further decomposed into other possible spatial components, such as fine fuel spatial pattern and unmeasured edaphic conditions.

No attempt was made in this study to determine “the” single model responsible for natural disturbance boundary creation. It was explicit in the analysis that there is no need to do this and that it is unlikely that a single mechanistic hypothesis would have been supported at all sites. Each fire and MPB event may be driven by a unique set of mechanistic factors. Thus, the initial goals of this study were not to indicate that one model was supported for fires and perhaps another was supported for MPB sites; rather, this was an attempt to quantify how often, on a landscape, a given model or factor is important for boundary creation.

3.4.3 Conclusions

All fire and MPB boundaries sampled here showed an influence of the abundance of susceptible hosts. Furthermore, seven out of eleven MPB boundaries showed only an indirect spatial pattern, acting through abundance of susceptible hosts. All fire boundaries maintained a direct influence of space indicating that in addition to the abundance of susceptible hosts, transient variables with a spatial trend, such as weather events, and unmeasured variables, such as soil moisture, were needed to explain a portion of the boundary formation. Multiple case study analysis such as that presented here is a powerful inference tool in studies where sample sizes are not sufficient to perform standard statistical tests. Furthermore, these results that address proportion of occurrence on a landscape—e.g., how often tree related factors influence the boundary, how often other spatial factors influence the boundary, how often aspect influences the boundary—can then be put into stochastic mechanistic simulation models to parameterize the stand-level details of the boundary. Not only does this type of analysis admit that processes in nature are fundamentally variable in the factors that influence them, it embraces

this variability in a way that is useful for further analysis and simulations. Boundaries are very biologically rich areas on the landscape, and an understanding of the factors—their frequency and their strength—that influence how they are created has been lacking.

Chapter 4 Complex Dynamics of Early Forest Succession At The Boundaries Of Wildfires And Mountain Pine Beetle Outbreaks

4.1 Introduction

Boundaries are important in landscapes because of their diverse structures and diverse functions, acting as filters and barriers to species movements and climatic variables, as well as sources, sinks and habitat for many species (Forman 1995). In general, most boundaries studied in ecology have been hard; inference about the structure and function of boundaries is likewise about hard edges. This preponderance of research on hard edges may be, in part, due to the abundance of hard boundaries created by forest management. In contrast, however, this thesis has demonstrated that forest boundaries created by natural disturbances may be both soft and hard (indeed, boundary contrast appears to be a continuum; Chapter 2). That boundaries can have dramatically different functions is known (Fagan et al. 1999). What is not known is whether soft boundaries have unique features since very few studies have examined the ecological consequences of this spatial complexity. In particular, the forest successional trajectories in complex boundaries are largely unknown.

An increasing number of ecological studies have demonstrated that the effects of disturbances on forest stand dynamics are more complex than “stand replacing” or “stand maintaining” (Noble & Slatyer 1981; Abrams & Scott 1989; Clark 1991; Sprugel 1991; Glenn-Lewin & van der Maarel 1992; Steele 1994; Attiwill 1994b; Minnich 1998; Maily et al. 2000; McIntire et al. 2001; Gilbert et al. 2003). Moreover, forest succession may proceed in several different pathways within the same disturbed patch because of the variation in disturbance severity within the event. Similarly, boundaries will likely have a large range of variation—from the most severely disturbed patches within the disturbance to the areas that are completely outside of the disturbed patch. These boundaries will have intermediate levels of tree mortality and overall disturbance severity and may have different successional trajectories than adjacent areas. To date, no study has described the early successional trajectories in boundaries, particularly in relation to the adjacent forested stand and disturbance core. This description of successional trajectories in natural disturbance boundaries represents the first goal of this study.

In addition to descriptions of successional trajectories, however, understanding the processes that generate the regeneration patterns is important for understanding regeneration. Four primary and proximate factors responsible for spatial natural regeneration patterns are light, seed source, seed bed, and competition for space (Lavender et al. 1990; Greene et al. 1999). Causal models—or path models—are hypotheses where the relationships between variables are posited to be unidirectional, or asymmetric, and can be generated with external information regarding causality. Setting up multiple *a priori* hypotheses that test for the relative influence of these factors allows for strong inference (Burnham & Anderson 1998). This study uses several *a priori* path hypotheses based on these four factors to test regeneration dynamics at the boundaries. Here, trees species have been grouped into ecologically similar types based on light requirements (shade tolerant and shade intolerant).

There are two primary objectives of this chapter. The first objective is to describe and compare the early successional trajectories of three fine scale spatial zones that occur at the boundaries of wildfires and MPB outbreaks—the disturbance core, the boundary, and the intact forest. Within the first objective, several details are of particular interest. While boundary zones are defined as having intermediate mortality, are the successional trajectories that result from the disturbance also intermediate? If they are not intermediate, do these boundary zones have successional trajectories that may lead to locally different forests as characterized by species composition, understory and overstory structure and successional sequence? The second objective is to use *a priori* spatially explicit causal models (Figure 4.1) to test the relative contributions of several factors that may have generated the natural regeneration patterns. Within this second objective, there are an additional set of questions. How important are the influences of seed source, seedbed, overstory tree abundance (acting as a surrogate for light), and plant competition to natural regeneration across the complex boundaries? Do shade tolerant and shade intolerant regeneration and understory advanced regeneration have different responses to these factors? Finally, by inference, the chapter concludes with a discussion of the implications of these data for simulation modeling and of simplifying a landscape by having primarily hard forest stand boundaries.

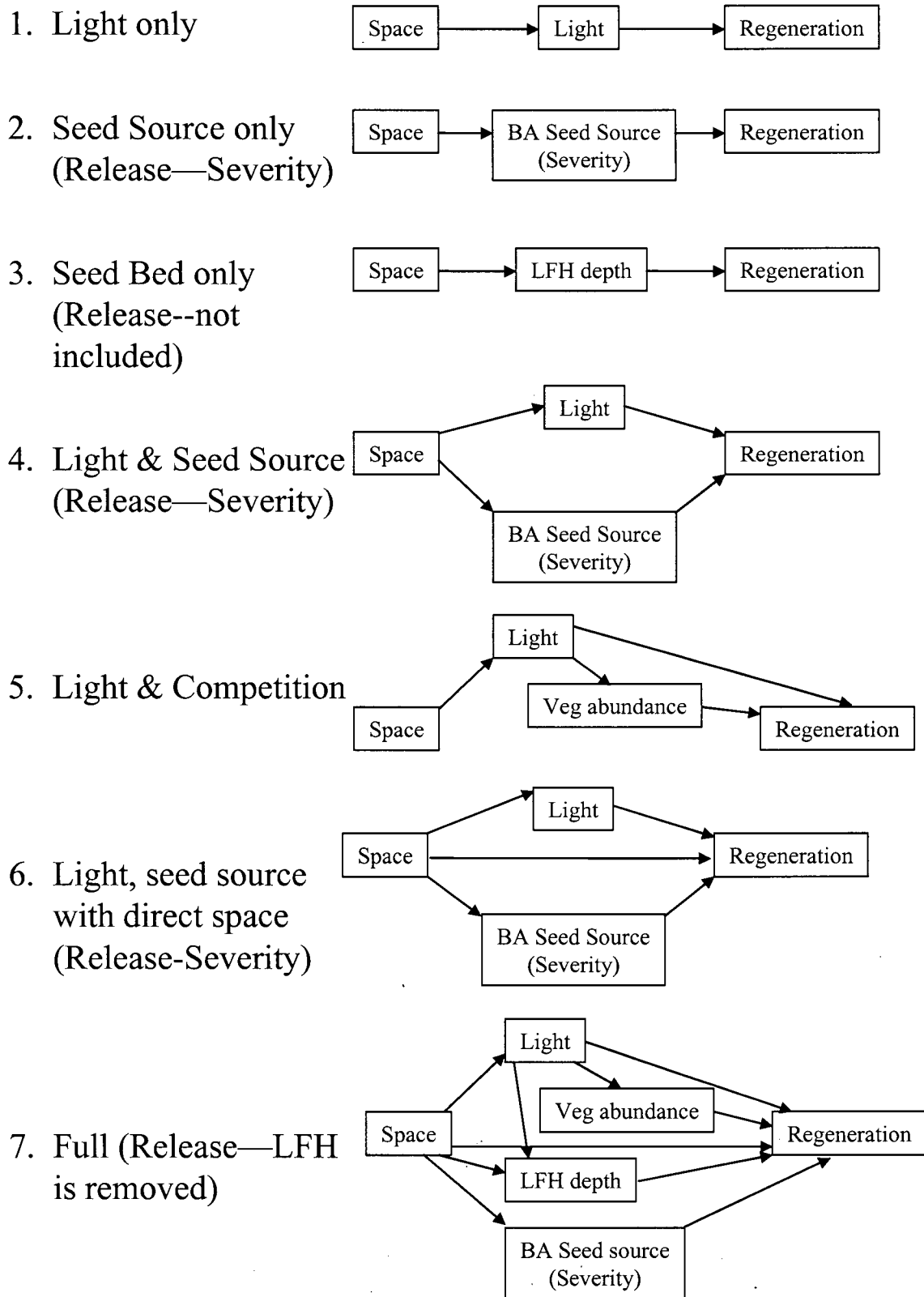


Figure 4.1. Path models. Note for analyses on advanced regeneration growth release (Release) the variable Seed Source is replaced throughout with Severity and LFH depth is removed.

4.2 Methods

4.2.1 Field Sampling

4.2.1.1 Study Area and Study Design

Details of the research area and study design are reported elsewhere (see Chapter 2). Research was conducted in the Arrow Lakes and Kootenay Forest Districts, in south central BC, Canada within three biogeoclimatic subzones (ICHmw2, ESSFwc1, and ESSFwc4 (Meidinger & Pojar 1991)). All mountain pine beetle (MPB) sites were dominated by lodgepole pine (*Pinus contorta*) and fire sites were dominated by lodgepole pine, subalpine fir (*Abies lasiocarpa*), white X Engelmann spruce hybrids (*Picea engelmannii* X *P. glauca*), or Douglas-fir (*Pseudotsuga menziesii*). These subzones are characterized by stand replacing fire disturbance regimes, with frequencies ranging from 150 years to 400 years (NDT 1 and 2; rare or infrequent stand initiating events) (Ministry of Forests & Ministry of Environment 1995).

In the summer of 2001, seven two-dimensional sampling transects were from five different fires (sites 12 and 20, and 17 and 21 were from the same fires, however, the transects were separated by at least 1 km from each other). All disturbances occurred between 1993 and 1997. Fires sites were lightning caused, had extensive areas that were not salvaged, were physically capable of being sampled (i.e., no slopes $>50^\circ$), occurred at elevations between 1400m and 1900m, and were in the province's fire database (Protection Branch 2001). All fires had active fire suppression efforts, however, site selection within each fire was constrained to sites where there was no or minimal evidence of local suppression efforts (e.g., palaski lines, red retardant embedded in down wood, evidence of trees cut during the fire). Fire boundaries examined in this study were along the side flanks of the fire event that moved up the slope and were located horizontally across the mountain slope. Eleven MPB sites had the following characteristics: mature stands (60 years $<$ tree age at DBH $<$ 150 years); canopy trees at least 20 cm, DBH; southerly aspect slopes (97° to 256°); elevation between 1150m and 1550m. MPB stands were overall of similar character due to the selective nature of the insect disturbance (mature lodgepole pine), though the secondary tree species and understory vegetation were not necessarily similar throughout. Placement of transects was random within a given disturbance boundary (see Chapter 2).

Sampling occurred using 2-dimensional sampling transects that ranged from 60m to 170m long and 40m to 60m wide. Transect length was determined on a site-by-site basis to encompass both the peak severity of the disturbance event and an area outside the mortality. Plots within each transect were contiguous and were 10m X 10m (100m²). Sites used in this study for both fire and MPB represent a full census of those that were accessible to sampling, given the sampling area and identified populations. Space was modeled as a one-dimensional variable (i.e., the long axis of the transect). This simplification was used for several reasons. It was decided based on the analysis of two-dimensional data reported in Chapter 2 that the longitudinal trend could be approximated using the single long axis. Furthermore, given the sample sizes at each site, the addition of the latitudinal variable increased model variance (uncertainty) and reduced degrees of freedom with very little added information.

4.2.1.2 Advanced Regeneration Growth Release

Within each 10mX10m plot, one randomly chosen tree sapling (50cm to 3m height) was selected and a cross-sectional disk was taken just above the ground. If a plot had no advanced regeneration, it was represented as a missing data point. Disks were sanded with 120 grit paper, and then two shallow, radial cuts were made with a sharp utility knife to clearly expose the ring boundaries. The first cut was made along the widest axis, and the second cut was made perpendicular to the first. All measurements were taken using a compound light microscope at 30 X magnification interfaced to AGRMM RINGSCAN program. In a few cases where it was not possible to read a perpendicular transect due to damage or other factors, another random angle was selected. Area increment was calculated based on the assumption that the two radii represented the two axes of an ellipse. Growth release was calculated as the ratio of the average annual area growth in the years following the disturbance up to present to the average annual growth in the 10 years immediately prior to the disturbance event. Growth release was log transformed in all analyses.

4.2.1.3 Field Measurements

A 10m² circular plot was placed in the center of each 10m X 10m plot and all occurrences of seedlings from 5cm to 50cm in height were counted. The lower height limit was placed to reduce errors associated with the detection of germinants. It is unlikely that all seedlings in this size range regenerated after the disturbance. Seedlings in this range, however,

will have survived the conditions since the disturbance and are thus considered a good representation of the regeneration process.

All trees greater than 10cm DBH, dead and alive, were measured for diameter at breast height (1.3m) and the cause of death (i.e., the disturbance event or other) was determined wherever possible. Basal area was calculated for each plot. Seed source was the basal area of living trees by shade tolerant or shade intolerant class. In addition, fire killed lodgepole pine trees were included in the seed source because of their semi-serotinous cones.

Light was estimated in the field in two ways: visual percent cover of overstory trees and basal area of living trees. These two variables were highly correlated. Neither of these is a perfect measure of light, though the latter is thought to be a more precise (repeatable) measure of available light. In this study, a surrogate of light is represented as the basal area of living trees and is written as “light(sur.)”. As a result, light(sur.) and seed source may covary. All models with these two variables have an explicit covariance modeled (through the space variable) to account for any covariation.

Competition was measured as the leaf area of all understory vegetation. Percent vegetation cover was estimated visually in the 10m² plots by species in three layers—herbs, shrubs below 2m and shrubs above 2m. These percentages were summed across species and across layers and divided by 100 to represent leaf area of the understory vegetation. In addition, vegetation community was measured using the first axis of a detrended canonical correspondence analysis on all layers of vegetation percent cover by species (ter Braak & Smilauer 1999).

Seedbed was measured as the depth of the LFH layer (in cm) at a random point within the regeneration plot.

4.2.2 Vegetation Description and Successional Trajectories

In these descriptions, I use the maximum boundary zone widths (calculated in Chapter 2 and referred to as MaxBZ). All but two boundaries (F18 and F19) were best described using three zones: the core of the disturbance, the boundary zone, and the intact forest¹⁰.

¹⁰ For purposes of terminology, this indicates that F18 and F19 are “hard” edges and the rest are softer.

To describe canopy trees, saplings, natural regeneration and vegetation in each of the three zones (disturbance core, boundary zone, and intact forest), several factors were measured and compared. Since the zones do not necessarily have equal sample sizes across a given boundary, these comparisons by zone will reflect this sample size disparity. First, the amount of remaining live basal area was quantified in each zone and compared to the original live basal area of that zone to quantify mortality. Second, the live basal area of plots within each zone was compared to zero to determine whether all trees were dead in the zone. Third, the understory advanced regeneration cross-sectional area growth was calculated for each zone and compared to the 10 year cross-sectional area growth immediately before the disturbance to quantify growth release of the pre-disturbance understory. Fourth, the abundance of natural regeneration was measured (classified into two levels of shade tolerance) and compared to the abundance of natural regeneration in the intact forest zone. Fifth, the understory vegetation cover was compared to that of the intact forest. Finally, the understory vegetation community was compared to the intact forest. For this, multivariate data were analyzed using detrended canonical correspondence analysis (DCCA) and only the first axis was used (ter Braak & Smilauer 1999). All comparisons were statistical and significance for all questions was set to $p=0.01$. Comparison of BA alive before and after was examined using paired t-tests (Proc ttest (SAS Institute Inc. 2000)). Examination of advanced regeneration growth release was examined using t-tests with $H_0=1$. Natural regeneration abundances, vegetation cover, and vegetation community were each compared across the three zones using generalized linear model ANOVAs (Natural Regeneration: Proc GENMOD, log link, negative binomial distribution to reflect count data and lsmeans option; Vegetation Cover and Vegetation Community: Proc GENMOD, log link, lsmeans option (SAS Institute Inc. 2000)).

To further characterize and summarize the vegetation patterns into successional trajectories described as either stand replacing, stand maintaining, stand accelerating or stand altering, a flow chart of binary responses was created (Figure 4.2). The first three of these terms have been used in other succession research and these have been interpreted here with quantitative definitions (Figure 4.2). As with any binary sequence of questions (e.g., strong inference by Platt (1964)), the order of the questions is not only influential, it largely determines the outcome; earlier outcomes are more likely to occur. In the sequence of questions used in this study, the three outcomes representing the least departure from standard successional

terminology—stand replacing, stand maintaining, or stand accelerating—are the earliest outcomes. Departures from these are later questions. Some of the outcomes are more similar ecologically to each other than others. For instance, “Stand Maintaining” and “Stand Altering 1” are similar, as the latter appears to represent a type of small gap dynamics. Furthermore, early questions in the flow chart are questions that do not depend on comparisons with the intact forest. All questions related to basal area (BA) are either compared to the BA alive at the time the disturbance occurred, or are compared to zero. Questions related to understory release are related to unity, being the absence of growth release. All questions related to vegetation and natural regeneration are compared to the intact forest, as this is the best alternative for comparison. Thus, differences between “Stand Altering 2” to “Stand Altering 6”, inclusive, rely on imperfect comparisons.

4.2.3 Regeneration Hypothesis Testing

I used path models (Figure 4.1) and a multiple hypothesis framework for analysis of natural regeneration data (Chamberlain 1890; Anderson et al. 2000; Zucchini 2000; Anderson & Burnham 2002). Specifically, regeneration was modeled in three separate analyses: shade intolerant natural regeneration, shade tolerant natural regeneration, and advance regeneration understory growth release. Shade intolerant species consisted of lodgepole pine (*Pinus contorta*), whitebark pine, western larch (*Larix occidentalis*), and Douglas-fir (*Pseudotsuga menziesii*), while shade tolerant species included western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), hybrid spruce (*Picea glauca X engelmannii*), and subalpine fir (*Abies lasiocarpa*). There were occasional hardwoods (trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) and these were included in the shade intolerant group. These groupings were based on the silvics of North America (Burns & Honkala 1990). While the light-related dichotomy is not absolute in nature, these groupings have numerous common features such as seed size and ability for seedlings to grow in low light conditions¹¹, though there are exceptions. All analyses were done three times, once for each group.

A priori path models were used and assessed for absolute fit (using CFI and RMSEA—derivations of the maximum likelihood goodness-of-fit statistic (Bentler 1990; Browne &

¹¹ Since regeneration included seedlings >5cm in height, this study does not explicitly infer to germination or seedling establishment.

Cudeck 1993)). A model was considered “good fitting” if it has either $CFI > 0.95$ or $RMSEA < 0.06$. Then “good” fitting models were compared using a relative measure of fit adjusted for small sample sizes (AIC_c see Akaike (1987); Burnham & Anderson (1998)).

In a multiple hypothesis framework, inference is only as strong as the models being tested. Where more than one model was selected by the data, parameters were estimated by using all “good fitting” models, weighted by their relative level of support (Burnham & Anderson 1998). Sites were not explicitly used as replicates of one another (see Chapter 3). Rather than suggest that all sites are affected by the same causal hypothesis, results are summarized to show the proportion of the sites for which a factor is important in understanding the regeneration pattern.

Natural regeneration is thought to be a direct and primary function of light, seed source and seedbed, while competition for space from other plants may be moderating factor. Other factors such as moisture and nutrients may also be important but were not modeled here. In the Arrow lakes, moisture is generally thought not to be a strong limitation to regeneration. Nutrients are generally thought to become limiting as the trees grow larger and have more competition between them. Throughout, space is modeled as a single variable representing the long axis of the boundary transects.

Seven path models were used for natural regeneration seedlings and six were used for advanced regeneration growth release (Figure 4.1). *A priori* logic for selection of these models follows. All models include a variable representing spatial position along the transect since it is unlikely that space will not influence the regeneration pattern, and spatial association must be explicitly modeled to account for lack of plot independence. There is one model for each of the three individual direct factors (Models 1, 2, and 3). When competition is included, it is always modeled to be directly affected by light, which in turn directly affects regeneration pattern (Models 5 and 6). No model is proposed in which competition is the only factor because it acts secondarily to the primary factors involved in seedling establishment. In contiguous forest, it has been proposed that seed source may not be an important factor (K.A. Klinka, pers. comm.), so Model 6 represents the full scenario without seed source. Light is thought to be important (Lavender et al. 1990), so it is included as a direct effect on regeneration in all models except 2 and 3. Model 4 is included to represent a seed source and light hypothesis that represents a combination of particularly influential factors at the boundary of a disturbance event (Greene &

Johnson 1996). A full model is included for completeness, but is not expected to perform well given the number of parameters. In addition, at some sites, the number of plots is statistically too small to perform tests on this full model (5 regressors).

Advanced regeneration growth release was not expected to be affected by seed source, nor by depth of forest floor to mineral layer. Furthermore, because the advanced regeneration was present on site before the disturbance, disturbance severity is included as a modeled variable. This was estimated as basal area killed by the disturbance. This variable may be correlated to light(sur.) and any covariance is explicitly modeled to account for this.

Model analysis was performed using AMOS structural equation model software (Arbuckle 1999; Byrne 2001). AIC_c is based on Akaike's original formula for AIC in the context of factor analysis (Akaike 1987) and is calculated external to the software as:

$$AIC_c = \chi^2 - 2 \cdot d.f. + \frac{2K(K+1)}{n-K-1}$$

where χ^2 is the chi-squared discrepancy, d.f. is the degrees of freedom of the model (total number of parameters in the model minus the total number of estimated parameters), K is the number of parameters and n is the sample size. This calculation is used throughout this paper for model comparison.

Akaike weights (Δ_i) and normalized Akaike weights are presented (w_i) (see Anderson et al. 2001). In general, where $\Delta_i < 3.8$, the models can be considered to have equivalent support, where $3.84 < \Delta_i < 7$ to 10, the models may have support, however, it is unlikely. Below these values, it is highly improbable, given the data, that the model describes the data. To account for model selection uncertainty (i.e., where several models have similar probabilities of being the "best" candidate model), parameter estimates presented here are averages from all models in which the parameter occur, relativized to the level of support for each model (Burnham & Anderson 1998).

All data presented from path analyses use normalized variables (mean=0, variance=1) and represent correlation coefficients ("r") between the variables. All analyses are tested for multivariate normality prior to analysis (Mardia 1970; Arbuckle 1999). Some sites fulfilled strict multivariate normality for each path model. Since the response variable in all cases is count data and likely comes from a negative binomial distribution, all parameter estimates and significance

levels are taken from bootstrap estimates and distributions, rather than the maximum likelihood estimates.

4.3 Results

4.3.1 Vegetation Descriptions and Successional Trajectories

In all but one site (M2), the boundary zones had statistically detectable mortality (Table 4.1). Two MPB sites (M13 and M16) and all but one of the fires (F18) showed total overstory mortality in the disturbance cores. Growth release of understory advanced regeneration occurred in all three zones, not only the boundary zones or disturbance cores. Vegetation cover was greater in the boundary zones than in the intact forest at 6 of 11 MPB and 3 of 5 fires sites. The vegetation community in the boundary zones is generally similar to that of the intact forest with only 3 of 11 MPB sites and 2 of 5 fire sites showing a difference. The measured variables (overstory mortality, sapling growth release, understory vegetation and natural regeneration), when examined as a group, were different in each boundary zone than in either the intact forest or disturbance core.

Of the 11 MPB sites, eight of the boundary zones had successional trajectories that were different from *both* the intact forest and the disturbance core (Table 4.2). Intact forest in all but one case was in either a “Stand Maintaining” condition or a “Stand Altering 1”. The intact forest at M16 had some overstory mortality, but no understory response, creating a thinned and changed forest with no successional dynamics expected.

Most (8 of 11) of the MPB boundary zones showed “Stand Acceleration”, and the others were either unaltered, had a semi-open canopy with a strong understory vegetation component or a shade intolerant regeneration under a semi-open canopy. None of the unaffected forest sites could be described as “Stand Accelerating”. All five fires had distinct boundary zones. The five fire boundaries all had semi-open to open canopies, with shade intolerant regeneration (“Altering 3”), shade tolerant regeneration (“Altering 4”), or intact advance regeneration with growth release (“Release 2” and “Accelerating”).

At least one core area of the MPB sites was described by each of the stand descriptors: stand replacing, maintaining, accelerating or altering. Six of the seven fires disturbance cores were described as stand replacing with no advanced regeneration.

4.3.2 Natural Regeneration and Understory Growth Release

AIC_c values demonstrate that at many sites, multiple models (up to 5) describe the data equally well (Table 4.3 to Table 4.6). Conversely, all sites had at least one good fitting model for at least one of the regeneration types and ¼ of all site tests had only a single good fitting model (no model uncertainty). The three simplest path models (Models 1, 2 and 3) all performed very well at many of the sites (based on having AIC_c differences within 3.84 of the best fitting model). Furthermore, Model 6—with the inclusion of a direct effect of space with light(sur.) and seed source—also performed well at numerous sites. Model 5 (light(sur.) and competition) performed very well at many sites. The full model was never selected. No one model fit well at more than 6 MPB sites (55%).

Shade intolerant regeneration generally was more predictable than shade tolerant regeneration across the boundary (Table 4.7). Parameters estimated from path models and weighted AIC_c values (

Table 4.6) demonstrate that light(sur.) was very important for understanding the pattern of shade intolerant regeneration (100% of fires sites and 54% of MPB sites) and much less important for shade tolerant regeneration (28% for fire, 30% for MPB—see Table 4.8). All relationships with light(sur.) (BA Alive) were negative, indicating that regeneration and growth release increases with decreasing basal area of living trees. Shade intolerant regeneration also showed a negative relationship with LFH depth in three MPB sites and shade tolerant in two MPB sites (Table 4.7). One fire site (F21) demonstrated a positive relationship between LFH depth and shade tolerant regeneration.

Neither seed source nor competition from understory vegetation was an important factor in understanding regeneration (Table 4.8). Seed source, as estimated by the basal area of shade intolerant or shade tolerant trees was not important at any site. Competition from understory vegetation was only important at one site, and the relationship was positive.

Both light(sur.) and disturbance severity were important variables for describing understory growth release, particularly in MPB sites (Table 4.7). Light(sur.) was a better predictor in MPB sites and severity performed better in fire sites. Growth release in intact forest, boundary zones and disturbance cores ranged from 1 to 8, 2 to 13, and 2 to 17, respectively.

Space was both an important indirect and direct variable at these sites (Table 4.7 and Table 4.8). Space directly influenced natural regeneration types, particularly shade intolerant regeneration, but was not very important in advanced regeneration. Space was an indirect factor most often for shade intolerant regeneration.

Overall, suitable parameters (at least one significant standardized regression coefficient) were found at five of seven fire sites and at ten of eleven MPB sites. By regeneration type, shade intolerant regeneration had significant modeled parameters in ten of 13 sites (77%), shade tolerant regeneration in nine of 17 sites (53%), and understory release in ten of 18 sites (56%). By predictor, light was significant at 13 of 18 sites (72%), seedbed in five of 18 sites (28%), severity in four of 18 sites (22%), and direct space at seven of 18 sites (39%).

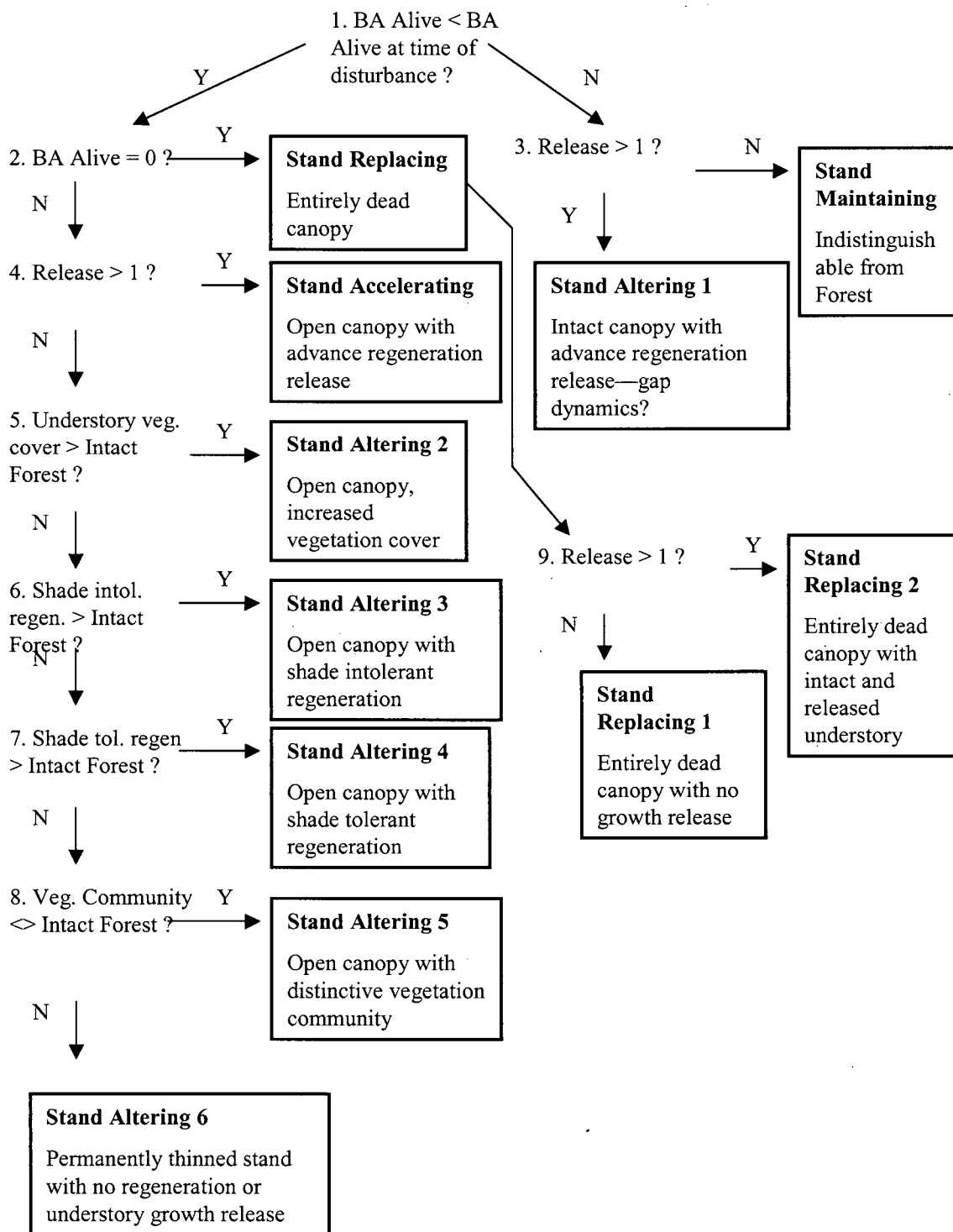


Figure 4.2. Flow chart of successional descriptions used in this paper. Release indicates advanced regeneration growth release (see text). Questions 1, 2, 3, 4 and 9 do not require comparison with the intact forest as a control. Demarcation for questions was $p < 0.01$. See Table 4.1 for complete results.

Table 4.1. Summarized results of statistical tests used to characterize the state of the overstory and understory trees and vegetation for all sites. Test significance levels are set to $p=0.01$. “N” and “Y” indicate non-significance or significance, respectively. “IF”, “BZ”, and “DC” indicate intact forest, boundary zone and disturbance core, respectively. See text for details for each statistical comparison.

Site	Zone	BA alive < BA alive at time of disturbance ?	BA Alive = 0?	Understory growth release >1?	Shade intolerant regeneration > IF ?	Shade tolerant regeneration > IF ?	Understory vegetation cover > IF ?	Vegetation community (1 st axis of DCCA) <> IF ?
M2	IF	N	N	Y				
	BZ	N	N	N	N	N	Y	N
	DC	Y	N	N	N	N	Y	N
M3	IF	N	N	N				
	BZ	Y	N	N	Y	Y	Y	Y
	DC	Y	N	Y	Y	N	Y	Y
M5	IF	N	N	N				
	BZ	Y	N	Y	Y	N	Y	Y
	DC	Y	N	N	Y	N	Y	N
M6	IF	N	N	Y				
	BZ	Y	N	Y	Y	Y	Y	N
	DC	Y	N	Y	Y	Y	Y	N
M8	IF	N	N	Y				
	BZ	Y	N	Y	N	Y	N	N
	DC	N	N	N	N	N	N	Y
M9	IF	N	N	N				
	BZ	Y	N	Y	N	Y	N	N
	DC	Y	N	N	N	Y	N	N
M10	IF	N	N	N				
	BZ	Y	N	N	Y	N	N	Y
	DC	Y	N	Y	N	N	N	N

M13	IF	N	N	Y				
	BZ	Y	N	Y	N	N	N	N
	DC	Y	Y	N	N	Y	N	N
M14	IF	N	N	Y				
	BZ	Y	N	Y	N	Y	Y	N
	DC	Y	N	Y	N	Y	Y	N
M15	IF	N	N	Y				
	BZ	Y	N	Y	Y	N	N	N
	DC	Y	N	Y	Y	N	N	N
M16	IF	Y	N	N				
	BZ	Y	N	Y	N	Y	Y	N
	DC	Y	Y	Y	N	N	Y	N
F11	IF	N	N	N				
	BZ	Y	N	N	N	Y	Y	N
	DC	Y	Y	N	N	Y	Y	N
F12	IF	N	N	Y				
	BZ	Y	N	N	N	Y	N	Y
	DC	Y	Y	N	N	Y	N	N
F17	IF	N	N	Y				
	BZ	Y	Y	Y	N	N	N	Y
	DC	Y	Y	N	N	N	N	Y
F18	IF	N	N	N				
	BZ	--		--	--	--	--	--
	DC	Y	N	N	Y	N	N	Y
F19	IF	N	N	N				
	BZ	--		--	--	--	--	--
	DC	Y	Y	N	N	N	N	N
F20	IF	N	N	N				
	BZ	Y	N	N	N	N	Y	N
	DC	Y	Y	N	N	N	N	N

	IF	N	N	Y				
F21	BZ	Y	N	Y	N	N	Y	N
	DC	Y	Y	N	N	N	N	N

Table 4.2. Successional trajectories following natural disturbances in the remaining intact forest, the boundary zone, and the disturbance core. Noted is when the boundary zone is different from both the intact forest and the disturbance core. These results are based on the dichotomous key in Figure 4.2. Sites F18 and F19 had no detectable boundary zone.

Site	Successional Trajectory			Boundary Trajectory Different?
	Intact Forest	Boundary Zone	Disturbance Core	
M2	Altering 1	Maintaining	Altering 2	Yes
M3	Maintaining	Altering 2	Accelerating	Yes
M5	Maintaining	Accelerating	Altering 2	Yes
M6	Altering 1	Accelerating	Accelerating	No
M8	Altering 1	Accelerating	Maintaining	Yes
M9	Maintaining	Accelerating	Altering 4	Yes
M10	Maintaining	Altering 3	Accelerating	Yes
M13	Altering 1	Accelerating	Replace 1	Yes
M14	Altering 1	Accelerating	Accelerating	No
M15	Altering 1	Accelerating	Accelerating	No
M16	Altering 6	Accelerating	Replace 2	Yes
F11	Maintaining	Altering 3	Replace 2	Yes
F12	Altering 1	Altering 3	Replace 1	Yes
F17	Altering 1	Replace 2	Replace 1	Yes
F18	Maintaining		Altering 2	N/A
F19	Maintaining		Replace 1	N/A
F20	Maintaining	Altering 4	Replace 1	Yes
F21	Altering 1	Accelerating	Replace 1	Yes

Table 4.3. Path model results for shade tolerant regeneration species. Numbers represent AIC_c differences (Δ_i). Bold= $\Delta_i < 3.84$, underline=CFI>0.95, *=RMSEA<0.06. # times best model is where $\Delta_i = 0.0$. # times <3.84 is where the path model is statistically indistinguishable ($P(\chi^2|3.84=0.05)$). # good models is where both Δ_i and either RMSEA or CFI were considered the path model good. K=number of parameters in the model.

				Shade Intolerant Path Model #							# good models
				1	2	3	4	5	6	Full	
Site#	N	Min AIC _c	d.f. K	1 5	1 5	1 5	2 8	2 8	1 9	6 15	
M2	44	0.9		0.0	0.5	0.6	6.1	10.2	4.3	30.5	0
M3	40	1.9		0.0	4.1	3.9	1.0	0.9*	3.0*	15.5	3
M5	68	1.1		1.1	4.5	3.5	49.0	0.6	0.0*	64.5	1
M6	48	4.0		0.0	2.0	0.8	27.2	8.4	5.2	43.2	0
M8	56	-0.8		0.0*	1.3	0.0*	17.8	1.7*	11.1	29.2	4
M9	60	-0.4		0.5*	0.0*	0.3*	8.1	0.8*	2.8*	11.3	5
M10	52	-0.3		0.9	2.3	0.0*	39.2	7.7	4.1	50.4	2
M13	48	0.0		0.0*	1.8	2.0	37.7	4.7	2.9*	47.5	2
M14	60	1.1		1.3	0.0	1.1	9.4	9.4	5.3	36.7	1
M15	56	1.9		2.2	3.9	2.9	31.3	2.8	0.0*	40.6	1
M16	56	-0.8		0.7*	0.4*	0.0*	3.8	20.0	4.3	30.4	3
# times best model				1	2	3	0	0	2	0	
# times within 3.84				5	4	4	1	3	5	0	
F11	48	-0.3		2.3	0.4*	0.0*	14.9	4.2	6.9	24.8	3
F12	64	-0.2		0.0*	8.1	8.5	16.7	21.5	1.7*	48.9	2
F17	60										
F18	24										
F19	40										
F20	44										
F21	52										
# times best model				1	0	1	0	0	0	0	
# times < 3.84				2	1	1	0	0	1	0	

Table 4.4. Path model results for shade intolerant species. See Table 4.3 for details.

		Shade Tolerant Path Model #									# good models
				1	2	3	4	5	6	Full	
Site#	N	Min AIC _c	d.f. K	1 5	1 5	1 5	2 8	2 8	1 9	6 15	
M2	44	2.7		0.0	0.5	0.5	8.6	11.0	2.5	39.6	0
M3	40	0.0		0.4*	0.5*	0.0*	15.4	1.3*	4.9*	33.6	4
M5	68	-0.7		1.0	0.0*	1.3	3.7	0.6*	1.8*	25.2	3
M6	48	-0.2		0.0*	1.1	0.1*	26.7	8.7	9.4	48.6	2
M8	56	-0.6		0.0*	1.7	0.2*	6.5	1.5*	10.9	26.3	3
M9	60	1.1		0.0	1.7	1.2	47.4	0.1*	1.4*	51.8	2
M10	52										
M13	48	-0.3		0.7*	0.3*	0.0*	2.5	4.2	3.2*	9.6*	5
M14	60	6.4		11.8	12.7	8.5	31.6	19.2	0.0	41.3	0
M15	56	-0.7		0.2*	0.1*	0.0*	15.5	0.7*	2.7*	54.3	5
M16	56	-0.2		1.0	0.0*	1.2	32.4	20.0	3.8	60.3	3
# times best model				2	2	3	0	0	0	0	
# times within 3.84				6	5	5	1	5	5	0	
F11	48	-0.6		3.4	0.3*	0.0*	4.1	5.1	7.1	17.7	3
F12	64	1.5		16.9	17.7	18.5	19.4	30.6	0.0*	39.8	1
F17	60	5.7		1.7	1.9	0.0	52.4	14.6	8.6	74.7	0
F18	24	8.6		1.6	0.0	0.0	9.1	5.9	3.1*	53.2	1
F19	40	4.0		0.2	0.8	0.0	15.3	9.6	5.5	44.1	0
F20	44	-0.4		0.0*	0.0*	0.1*	13.8	0.9*	5.5	27.5	4
F21	52	-0.6		0.0*	0.9*	0.4*	36.3	0.2*	7.5	43.1	4
# times best model				2	0	1	0	0	1	0	
# times < 3.84				3	3	3	0	2	2	0	

Table 4.5. Path model results for understory growth release. See Table 4.3 for details.

		Adv. Reg. growth release Model #								
				1	2	4	5	6	Full	
Site	N	Min	d.f.	1	1	2	2	1	3	# good
		AIC _c	K	5	5	8	8	9	12	models
M2	44	0.0		0.0*	0.0*	2.8	9.0	4.9	23.6	3
M3	40	0.2		0.1*	0.0*	3.4	1.1*	6.6	16.5*	4
M5	68	1.0		1.9	4.5	2.5	1.9	0.0*	14.3*	1
M6	48	2.8		0.3	6.2	1.7	9.8	0.0*	19.5	1
M8	56	1.1		4.3	0.0	2.1	5.0	2.5	15.5	1
M9	60	3.4		0.0	0.3	2.8	0.1	2.4	14.0*	0
M10	52	2.3		0.0*	0.5*	4.0	13.2	2.9*	26.6	3
M13	48	-0.6		1.2	0.0*	5.1	6.1	6.5	21.0	2
M14	60	1.1		4.5	0.0	10.2	9.8	5.9	28.7	1
M15	56	0.3		0.6	0.3	3.1	4.0	0.0	12.5	0
M16	56	8.3		0.0	16.7	13.7	15.7	7.5	41.4	0
# times best model				1	5	1	0	2	0	
# times within 3.84				3	6	2	2	4	0	
F11	48	1.9		4.2	3.3	3.6	4.7	0.0*	12.9*	1
F12	64	0.0		0.3*	0.0*	1.6*	14.8	3.9*	30.9	3
F17	60	2.2		0.5*	0.0*	0.3*	0.8*	3.0*	20.2	5
F18	24	1.9		0.0	6.9	4.8	4.5	6.1*	11.5*	0
F19	40	8.2		0.0	1.6	2.5	1.1	3.2	13.3*	2
F20	44	0.0		4.6	0.0*	5.8	5.2	8.4	31.3	1
F21	52	3.4		2.6	0.0*	4.3	2.6	6.8	18.1	1
# times best model				1	3	0	0	0	0	
# times < 3.84				3	3	2	1	0	0	

Table 4.6. Akaike weights, $w_i = \frac{\exp(-\Delta_i/2)}{\sum_{r=1}^R \exp(-\Delta_r/2)}$. These can be interpreted approximately as the probability that model is the best

model (Burnham & Anderson 2001). Weights >0.05 are indicated by bold typeface.

Site	Shade intolerant regeneration Model #							Shade tolerant regeneration Model #							Adv. Reg. growth release Model #						
	1	2	3	4	5	6	Full	1	2	3	4	5	6	Full	1	2	4	5	6	Full	
M2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.43	0.42	0.11	0.00	0.04	0.00	
M3	0.00	0.00	0.00	0.41	0.44	0.15	0.00	0.25	0.24	0.31	0.00	0.16	0.03	0.00	0.34	0.36	0.07	0.21	0.01	0.00	
M5	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.46	0.00	0.00	0.35	0.19	0.00	0.00	0.00	0.00	0.00	1.00	0.00	
M6	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.52	0.00	0.48	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	
M8	0.34	0.18	0.34	0.00	0.14	0.00	0.00	0.42	0.00	0.38	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	
M9	0.22	0.28	0.24	0.00	0.19	0.07	0.00	0.00	0.00	0.00	0.00	0.65	0.35	0.00	0.00	0.00	0.00	0.00	0.00	1.00	
M10	0.39	0.00	0.61	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.39	0.00	0.00	0.12	0.00	
M13	0.81	0.00	0.00	0.00	0.00	0.19	0.00	0.23	0.28	0.33	0.09	0.00	0.07	0.00	0.33	0.60	0.05	0.00	0.02	0.00	
M14	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	
M15	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.24	0.25	0.26	0.00	0.18	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
M16	0.27	0.31	0.38	0.00	0.00	0.04	0.00	0.35	0.57	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
F11	0.14	0.35	0.44	0.00	0.05	0.01	0.00	0.08	0.39	0.45	0.06	0.00	0.01	0.00	0.00	0.00	0.00	0.00	1.00	0.00	
F12	0.70	0.00	0.00	0.00	0.00	0.30	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.35	0.41	0.18	0.00	0.06	0.00	
F17								0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.28	0.25	0.19	0.06	0.00	
F18								0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.94	0.06	
F19								0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.26	0.00	
F20								0.28	0.28	0.27	0.00	0.18	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	
F21								0.29	0.19	0.25	0.00	0.27	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	

Table 4.7. Significant standardized coefficients (r) based on multimodel averaging, weighted by the relative (AIC_c) strength of the model. “—” indicates not sufficient regeneration counts to perform analysis. Veg. indicates competition from understory vegetation. Bold: $p < 0.01$; Not bold: $p < 0.05$.

Site	Shade intolerant regeneration						Shade tolerant regeneration						Advance regeneration growth release					
	Seed Source	Seed Bed	Light (sur.)	Veg.	Direct Space	Indirect Space	Seed Source	Seed Bed	Light (sur.)	Veg.	Direct Space	Indirect Space	Light (sur.)	Severity	Veg.	Direct Space	Indirect Space	
M2													-0.35					
M3			-0.34			0.19								0.54			0.33	
M5			-0.25		-0.23	-0.08		-0.1					-0.21					
M6													-0.39			0.3		
M8		-0.25						-0.26	-0.34			0.11						
M9			-0.27	0.14					-0.33									
M10			-0.39															
M13		-0.17	-0.22		0.15	0.13							-0.58					
M14													-0.45		0.28			
M15					0.28				-0.26									
M16		-0.27	-0.26								-0.3							
F11			-0.33		-0.37				-0.32		-0.44							
F12			-0.38			0.23					-0.72			0.44				
F17	—	—	—	—	—	—								0.37				
F18	—	—	—	—	—	—							-0.3				-0.26	
F19	—	—	—	—	—	—											-0.36	
F20	—	—	—	—	—	—								0.53				
F21	—	—	—	—	—	—		0.25	0.28									

Table 4.8. Proportion (and number) of sites that each relationship has a significant path coefficient on natural regeneration ($p < 0.05$) within a model that is selected as being the “best” models (based on AIC). This is equivalent to a significant regression coefficient in a multiple regression, but only from those models that are considered absolutely ($CFI > 0.95$ or $RMSEA < 0.06$) and relatively ($\Delta_i < 3.8$) good.

Relationship	Shade intolerant		Shade tolerant		Adv. Reg. Release	
	MPB	Fire	MPB	Fire	MPB	Fire
Seed Source	0%(0)	0%(0)	0%(0)	0%(0)		
Seed Bed	27%(3)	0%(0)	20%(2)	14%(1)		
Light	54%(6)	100%(2)	30%(3)	28%(2)	45%(5)	14%(1)
Severity					9%(1)	42%(3)
Competition	9%(1)	0%(0)	0%(0)	0%(0)	9%(1)	0%(0)
Direct space	27%(3)	50%(1)	10%(1)	28%(2)	9%(1)	0%(0)
Indirect space	27%(3)	50%(1)	10%(1)	14%(1)	9%(1)	28%(2)
Total	82%(8/11)	100%(2/2)	50%(5/10)	58%(4/7)	55%(6/11)	58%(4/7)

4.4 Discussion

In this study, complex 2-D structures of natural disturbance boundaries were found to lead to early successional trajectories that were different in time or in quality when compared to the intact forest or disturbance core. In spite of these boundaries being characterized by intermediate mortality from the disturbance events, the successional trajectories are distinct and not intermediate. The key variables that described the regeneration patterns—light, seedbed, and severity—were not strongly affected by the type of disturbance. More influential was the type of regeneration (shade tolerance and advanced regeneration). In Chapter 2, it was demonstrated that the boundary zone width ranged between 0m and 120m (average 30m-50m), representing between 15% and 30% of a hypothetical landscape. Since these boundary zones have different successional trajectories, naturally disturbed landscapes contain a large amount of spatio-temporal heterogeneity at a local scale that has not yet been appreciated.

4.4.1 Vegetation Descriptions and Successional Trajectories

Individual variables measured across a given boundary were similar between zones. However, when examined as a group, representing the overall response of the trees and understory vegetation, no boundary zone showed a similar pattern to either the intact forest or the disturbance core zones.

The differences in the successional trajectories of the three zones across the disturbance boundaries are non-trivial. The intact forest zones maintained their original successional trajectories but with some detectable understory growth release. The boundary zones all have a thinned canopy, leading to semi-open forest conditions. At two of the fire sites (F11 and F12), the boundary zones had an abundance of shade intolerant regeneration under a partial canopy, a relatively uncommon condition. Thus, while the canopy conditions are intermediate in the boundary zone, the understory is qualitatively different. This creates a more spatially diverse forest across the boundary than a simple disturbed/undisturbed condition.

Boundary zones in the MPB sites were primarily characterized as “stand accelerating”. Because the intact forest was in an early seral condition (lodgepole pine dominated), this boundary zone was clearly not intermediate between the intact forest and the disturbance. These boundary zones primarily had reduced canopy and had either shade intolerant regeneration, shade

tolerant regeneration or advanced regeneration growth release filling in the understory. In all three of these stand conditions, the resulting forest has structural properties and early temporal trajectories that were different than either adjacent forest zone. In cases where the boundary zone was not different from both the intact forest and the disturbance core (M6, M14, M15), there was usually low tree mortality in the disturbance core and boundary zone, making it difficult to distinguish forest characteristics in the three zones. Overall, non-linear consequences of disturbance induced partial overstory and understory mortality create these non-intermediate dynamics.

4.4.2 Natural Regeneration and Understory Growth Release

Of the variables modeled in this study, light(sur.), seedbed, and severity (for advanced regeneration) were most important for understanding regeneration patterns. Unexpectedly, seed source and vegetation competition had little support as determinants of natural regeneration. The elimination of variables can be of value for many scientific purposes, such as simulation modeling (see below) and determining priorities for research. As expected, light(sur.) was a more important factor on shade intolerant regeneration than shade tolerant regeneration. Furthermore, shade intolerant regeneration had a spatial trend across the boundary, as indicated by the direct and indirect influences of space, more often than shade tolerant regeneration. Consistent with the light requirements of these two groups, shade intolerant regeneration was more responsive to natural disturbance, which create a light environment that is suitable for germination, seedling establishment and seedling growth, than was shade tolerant regeneration. Understory growth release was best predicted by light(sur.) in MPB sites and severity in fire sites. These two variables are highly correlated; the former measured the presence of trees and the latter measured the absence of trees. The higher overall severity of mortality in fires may account for the greater predictability provided by severity as compared to light. Natural regeneration is notoriously difficult to model; the finding that there were suitable models at all sites and that there was predictability of regeneration at all but three sites indicates that the models used were adequate.

The use of a multiple hypothesis framework, where model comparisons determine demarcation, is a robust analysis strategy since the data are simultaneously confronted with alternate hypotheses (Anderson et al. 2000). Thus, if a hypothesis is selected as “good”, not only is it good in an absolute sense (i.e., standardized coefficients), but it is also “good” in a relative

sense. This multiple hypothesis framework does not rely on arbitrary rejection of hypotheses based on null hypotheses (e.g., $p < 0.05$); rather hypotheses can be rejected based on a series of viable hypotheses. A corollary to the notion of relative fit is that the “best” model is only the best, given the set of working models. Thus, the impact of unmodeled variables, such as moisture and nutrients, is uncertain. In this study, there was considerable model uncertainty, most likely because all models explicitly contained the variable “space” (space was an important influence on light(sur.), seed source and severity in all sites, data not shown). Where model uncertainty existed, model averaging was used to calculate parameters, embracing the uncertainty and making robust parameter estimates in spite of the uncertainty.

4.4.3 Space

Modeling space explicitly had two purposes. First, spatial independence of the data was required for statistical analyses but was clearly not present in this study so it was modeled explicitly. Second, space may be a factor that can lead to further inference. Space was detected to be a direct influence on regeneration at seven of 18 sites, leading to one of two interpretations. Space acts as a surrogate for unmeasured variables that have a spatial component to them. Variables such as moisture, nutrients, or microclimate that may also trend across the boundary could be detected in the spatial variable. Alternatively, a direct effect of space could represent a spatial lag in one or more of the variables. For example, seeds may be dispersed away from source trees, leading to an association with seed source, but with a spatial lag. This would create a spatial trend detectable across the boundary, but no significant association with seed source when analyzed using the methodology of this study. In either situation, knowing that space was important at approximately 40% of the sites indicates that, at these sites, there is more information contained in the data due to unmodeled factors. More effort is needed to explain this spatial trend, but, since it is only at 40% of the sites, it may not be necessary depending on future goals.

The difference between the indirect and direct influence of space lies in measured and unmeasured forest characteristics. When an indirect influence is detected, regeneration has a spatial component (i.e., a trend) across the boundary; however, it is adequately explained by other model variables. In Model 1 at site F12, for example, the indirect effect of space reflects the spatial trend in the light(sur.) variable and its effect on shade intolerant regeneration.

4.4.4 Implications

4.4.4.1 Landscape Modeling

There is considerable value in knowing *how often* a factor is important on a landscape, rather than just *whether* it is important or not. Clearly, seed source may be an important factor for natural regeneration and vegetation competition *potentially* has a deleterious impact for natural regeneration and advanced regeneration. However, in simulation modeling, each addition factor that must be parameterized creates more complexity, more effort, more error, and less generality. This study demonstrates that to understand regeneration in natural disturbance boundaries at sites like these in these landscapes, several factors may not be very important or are adequately represented by other factors. Inclusion of these factors in simulations of these landscapes may not improve predictive performance of natural regeneration dynamics and forest successional trajectories after disturbance.

This study suggests that light(sur.), severity, seedbed and space are the primary factors that should be included in simulation models to predict natural regeneration at natural disturbance boundaries. However, each of these factors is important at only a subset of my study sites. The number of sites at which a variable is determined to be important could be an estimate of the frequency of importance on the landscape for each factor. The differences between deterministic and stochastic models of boundaries in these landscapes would be large. Deterministic models would generally include all possible factors at their mean importance values whereas stochastic models would allow for some factors to not affect regeneration dynamics locally and at other locations to be the primary influence. Thus, rare events, such as competition being important at 10% of the simulated sites, could be periodically simulated, creating a diverse mosaic of processes across the landscape.

4.4.4.2 Long Term Dynamics

It is unclear what will happen to these boundary zones in the long term. If the early successional trajectory differences found in the boundary zones of this study were maintained over time, natural disturbance landscapes would persist with local regions of temporal and structural diversity. This local diversity would contribute to the regional diversity, creating a multi-scale successional complexity on landscapes. Alternatively, the edges of disturbances may

move with time due to windthrow, effectively eliminating the complexity created in the boundary zones in the four to seven years following the disturbances (the sampling window in this study). Furthermore, horizontal processes influencing the boundary zone from the disturbance opening, such as light penetration or microclimate, may continue to alter the boundary in unknown ways. Clearly, a similar analysis to the current study, but in much older disturbance events or using a chronosequence, or by using a simulation tool, would be necessary to answer these questions.

4.4.4.3 Forest Management

The natural disturbance paradigm states that, as a coarse filter approach to maintaining biodiversity on the landscape, forest management planning should be based on the spatial and temporal patterns of natural disturbance. Similar to wildlife tree islands created by fires, the generation of complex boundaries around harvested patches has the potential to alter species dynamics in ways that are more similar to NDs. The creation of hard edges in human managed landscapes may have resulted in dramatic simplification of landscapes in ways that have not yet been described. While this study demonstrated that complex natural disturbance boundaries lead to diverse successional trajectories in boundary zones, it is not certain that creating these types of boundaries would result in similar patterns in a harvested patch. Since light, severity and depth to mineral soil were the three strongest variables in the regeneration models, and these factors can be manipulated in a partial cutting pattern at the edge of a clear cut harvest patch, these successional patterns may be repeatable. If understory was left partially intact during the harvest, it may allow for similar dynamics to those detected in this study. Thus, creating spatial diversity in landscapes at the edges of harvested patches would lead to a greater diversity in local successional trajectories than is the case in hard edges. These, in turn, would lead to changes in species and forest structure over long periods that would be more similar to natural disturbances and increase local diversity.

4.4.5 Conclusions

Light surrogate showed a strong relationship with shade intolerant species, moderate relationship with shade tolerant and advanced regeneration. Seed bed was an uncommon factor in understanding natural regeneration in these sites (0% to 27% of sites for fires and MPB for both shade intolerant and shade tolerant). Seed source, understory competition, two factors that are

often claimed to be important for understanding regeneration, were not necessary to improve model fit. Boundary zones of the sites sampled here showed early successional trajectories that were not intermediate between the adjacent intact forest or disturbance core.

Chapter 5 General Discussion and Future Directions

5.1 Summary of Results

The chapters of this thesis have followed the general logic of: what and where are the boundaries? Why are they structured? What are the consequences of these boundaries for forest successional trajectories? Or: what, why and should we care? Below, I summarize the results of each chapter and link them to the objectives in section 1.2. These results are meant to be viewed only within the explicit constraints of the sampling space used in this study: all conclusions and inferences are made solely towards fires and MPB outbreaks that occurred between 1994 and 1997, on southerly facing aspects, fire flanks, that had detectable fire suppression, and that were in a narrow elevation range. Clearly, the patterns measured in this thesis apply only to the data collected for this thesis. Ultimately, these data may provide the best guess for inference beyond the sites in this study.

5.1.1 Revisiting Objectives

The first data chapter (Chapter 2) began by investigating a spatial technique for the objective description of complex disturbance patch boundaries: spatially-constrained clustering. Spatially constrained clustering is not a new technique in spatial analysis (Legendre 1986), but had not yet been applied to describing complex boundaries. Using two extremes of boundary width estimations (MaxBZ and MinBZ), I was able to objectively describe boundary width, sinuosity, steepness, and heterogeneity (objective Ch 2a). The technique identified spatial complexity at the boundaries of natural disturbances at several scales (5mX5m, 10mX10m, and 20mX20m). Boundaries examined were found to range from 0m wide to 120m wide, with means ranging from approximately 30m to 50m (objective Ch 2b). Of primary importance, these boundaries were shown to have a fine scale of heterogeneity and spatial diversity that was comparable to or higher than that of both the intact forest and the disturbance core (objective Ch 2b). While sample sizes were not large enough to make rigorous comparisons between wildfire and MPB boundaries, the variance in each of these boundary characteristics was high and overlapped at all scales (objective Ch 2c). The chapter concluded by demonstrating that in a hypothetical landscape affected by natural disturbances of a range of disturbance sizes that are

characteristic of the disturbances in the area studied, the boundaries would encompass from 10% to 30% of the surface area of that landscape.

Chapter 3 examined the potential factors affecting the mortality pattern across the boundaries. In conjunction with space as a modeled factor, the chapter demonstrated that 7/11 of the MPB outbreaks measured here stopped because of forest stand characteristics (objective Ch 3a), rather than any spatially constrained variable. Included in possible spatial variables is MPB dispersal. The potential implications of this result are dramatic because it suggests that to understand and predict MPB outbreaks in similar site conditions to those examined here, MPB population modeling may not be necessary in 7/11 of the outbreaks for direct estimation of the boundaries created by MPB outbreaks (objective Ch 3b). In contrast, all fires measured here exhibited a significant impact of space demonstrating that unmeasured spatial variables, such as weather, were influences in all sites. However, in every site, stand-level variables could account for a significant component of the boundary formation. Of primary importance at virtually all sites was the abundance of trees that are more susceptible to fire mortality (quantified by BA; objective Ch 3a). This has the implication that all fires and all MPB outbreaks measured in this area have been influenced by the landscape mosaic that was set up by past disturbances and environmental factors. That disturbances cease non-randomly is not a new concept, but it has not previously been reported that 100% of disturbance boundaries, and thus disturbance cessation, are at least partially driven by stand-level features. Furthermore, tree density, age, and aspect each had an effect on boundary creation at a small number of sites (objective Ch 3a). Thus, while the fingerprint model of past disturbance does not entirely drive current disturbances, but it does affect a portion of the landscape.

Chapter 4 demonstrated that complex boundaries do have ecological significance. The boundary zones have intermediate levels of tree mortality but this is not reflected in intermediate successional trajectories (objective Ch 4a). Because of the potential for a multitude of understory responses to disturbance severity, the boundaries contained forest zones with accelerated stand conditions, and several different levels of altered stand conditions. These alterations included unusual conditions such as shade intolerant natural regeneration growing in a zone of partial overstory mortality. This would result in a future stand similar to that expected from planting lodgepole pine in a selectively harvested cutblock. More generally, the boundaries examined demonstrated that even in "stand replacing" fires, there is the potential for a multitude of

successional trajectories around the periphery of the disturbance patch. Natural disturbances that would traditionally be seen as a single severity could now be viewed as mixed severity, if the boundaries are included. The spatial diversity that is added to landscapes because of these boundary conditions creates a higher degree of stand-level heterogeneity than has been so far described. Virtually no region of fire-driven landscapes would be devoid of this type of spatial heterogeneity, even those that are characterized by extremely large disturbances. The long term ecosystem consequences of replacing this type of spatial diversity by producing a harvested landscape with only hard edges are not known. Path models of natural regeneration and advanced regeneration showed relationships with a light surrogate and disturbance severity at numerous sites, relationships with seed bed at only a few sites, and relationships with understory vegetation or seed source at no sites (objective Ch 4b).

5.2 *Conclusions*

The MPB and wildfire boundaries studied here occurred along a continuum of hard to soft, ranging from 0m to 120m in width, with a mean of 40 to 50 m. This roughly translates to 14% to 30% of a landscape area in boundary zones (200ha and 40ha). This boundary complexity creates high landscape heterogeneity that we have been largely unaware of, or at least that we have ignored, if we already knew all of this. Virtually all natural disturbance boundaries examined were partly or wholly related to stand level characteristics. Finally, boundary zones of the natural disturbances sampled in this study have successional trajectories and regeneration patterns that are different compared to those in adjacent forests and disturbance cores. These early temporal trajectories are not intermediate between the forest stands on either side of the boundary zones.

5.3 *Is This New?*

Several components of this thesis are novel contributions to forest ecology and management.

First, this is the one of the first quantitative demonstrations of the softness or hardness of natural disturbance boundaries at the stand scale (see review by Kent et al. (1997) for a demonstration of this). Thus, while ecologists had informally recognized that natural disturbance boundaries are spatially complex, this had been poorly quantified.

Second, I sampled at multiple sites but I did not treat this as statistical replication. Instead, plot-level replication within sites acted as the scale of replication for analysis, and each site represented a case study. The success of this approach relies on two phenomena. First, processes that appear deterministic at one scale become probabilistic at a higher scale. Thus, rather than stratifying the population of disturbance sites to gain a precise mechanistic understanding (e.g., “this is an analysis of fire boundaries on 20° slopes, with 180° aspect, in 100% lodgepole pine forests, resulting from late summer fires that began at 1400m elevation...”), which becomes impossible in many landscape scale studies, this study provides a description of the range of conditions in a region (the ALFD). This study showed that 7/11 of the MPB disturbances in this area stopped due to forest characteristics, not due to dispersal limitation. Furthermore, too much stratification actually would have eliminated many of the factors affecting fire cessation. In the case of fire in this study, the abundance of susceptible trees affected fire boundaries. If I had stratified out boundaries that crossed stand types, I could not have observed this result. A further benefit of this approach is that it is not necessary that all sites follow the same mechanistic processes. At only one site, understory vegetation was shown to affect advanced regeneration growth release. In a replication-based sampling strategy, this result from this site would have been eliminated, and the general conclusion would be that understory vegetation did not significantly affect advance regeneration growth release. The conclusion here is that understory vegetation is important at a small subset of sites. This type of information should not be lost.

Third, this study combined three analysis techniques that have rarely been used together. I used 1) causal path modeling (e.g., Shipley 2000) with 2) space explicitly modeled (e.g., Zmyslony & Gagnon 2000) using 3) an *a priori* multiple hypothesis framework (see Burnham & Anderson 1998). While each of these techniques has been developed to expand inferences, the combination of the three is uncommon and proved to be very powerful. Landscape analyses often suffer from an inability to manipulate the variables of interest. The techniques I used here alleviated some of the inferential limitations.

Fourth, while disturbance initiation and propagation have been examined extensively (though not entirely resolved), the factors affecting the termination of disturbances are poorly understood (see MPB or Fire models, e.g., Logan et al. 1998; He & Mladenoff 1999). When disturbances are modeled, they are often stopped based on population-based parameters, such as dispersal distances, or are stopped probabilistically based on overall fire size (e.g., Finney 1999).

My study demonstrated that population-based parameters may not be useful at some sites, depending on the nature of the forest.

Fifth, one result from this study is the quantification of the impact of forest stand variables on the propagation on natural disturbances, which permits inferences about the impact of past disturbances on future disturbance events (see also Cumming (2001a)). The idea of disturbance fingerprints has been previously suggested (J.P. Kimmins, pers. comm.), and this study provides some minor support for this interpretation. In this study, fires and MPB each had one site that showed an effect of forest age—the most direct measure of past disturbance—on the current boundary. Furthermore, the amount of susceptible trees was a significant factor in the creation of the boundary in all but one of the disturbance events in this study.

Finally, few studies about natural disturbances have investigated more than one type of disturbance (see discussions in McCullough et al. (1998) and Edmonds et al. (2000) that demonstrate little overlap). Organisms have likely adapted to all of the natural disturbances in an area, not just the fires. In many fire habitats, multiple disturbance types occur, each contributing to the structural, functional and species compositions of the landscape. My study compared two dominant natural disturbances. As suspected, numerous features of these two disturbances were similar, including the influence of trees species on the disturbance boundary creation.

5.4 *Implications*

5.4.1 Ecological

This study described a feature of natural landscapes that occurs around wildfires and MPB outbreaks. It challenges the perception that edges are linear and narrow features on the landscape and merges the literature on gradients with that of forest edges (Kent et al. 1997), two fields that generally have different spatial scales of analysis. Gradients are often perceived to be at large spatial scales and edges at smaller ones. This study examined many types of edges of natural disturbances, including hard and soft edges.

The consequences of complex boundaries for organisms other than the tree species I studied have rarely been investigated. A small number of studies has demonstrated differences between soft and hard edges for a few species (e.g., birds (Ratti & Reese 1988), mammalian herbivores and predators (Forman 1995; Voller 1998)). It is known that many species require

multiple habitat features within close spatial and temporal proximity (Bowman & Harris 1980; Haila et al. 1994). In those places where dead wood can be sufficiently maintained, the application of complex boundaries in variable retention harvests, for example, may be beneficial. Furthermore, species that rely on understory vegetation and regenerating forests, such as mammalian herbivores, would possibly benefit from implementing these patterns. Plant and tree colonizations into openings would be altered, leading to increased seed sources if treed "peninsulas" were left into openings. Overall, however, the objectives of coarse filter strategies, like ENFD, are to protect and maintain biodiversity in ways and for species that we cannot entirely predict.

By reducing the relative abundance of natural disturbances in many landscapes using techniques such as fire suppression and replacing them with forest harvesting, these complex boundary habitats may be progressively eliminated. Thus, a shift from soft boundaries, which diversify the forest mosaic, to hard edges, throughout forest landscapes has likely already reduced spatial heterogeneity. This level of heterogeneity could likely be returned to these landscapes with changes in forest management.

5.4.2 Should Forest Management Create Soft Boundaries?

This thesis does not directly answer this question. The ENFD paradigm proposes that a coarse filter strategy for maintaining and conserving biological diversity is to emulate the patterns and processes of natural disturbances. If this paradigm is correct, then this thesis provides indirect data that suggests that spatially variable boundaries should be implemented in forest management designs. Wildfire and MPB disturbances created patterns of living tree structure that, at their boundaries, could be readily emulated and may have a beneficial role for some conservation goals. Ideally, studies should now be conducted comparing the impacts of soft and hard management-induced edges on a suite of species. These could be conducted in harvesting trials or experimental forests at first, and then implemented later in working forests. If management were to create complex boundaries, the boundaries in harvested patches would be more like those of natural disturbances and would likely result in higher levels of local heterogeneity than in conventional harvesting.

Other research unrelated to the ENFD paradigm has shown that many wildlife species require multiple habitats within relatively small spatial areas (e.g., home ranges), providing

independent support for the idea of complex boundaries (e.g., Haila et al. 1994). Chapter 4 demonstrated that these complex boundaries created different forests zones at the periphery of natural disturbance events as compared to the disturbance core or the intact forest. Forest harvesting could emulate the patterns observed in this study because the variables that were important for understory regeneration were light, disturbance severity and LFH depth. Since these could be reproduced by forest harvesting, it is likely that if boundaries of harvested areas were made more variable than they generally are, these forest responses would occur.

Several additional management benefits would result from following this ecologically-based suggestion. The visual quality of soft harvest boundaries for visually sensitive areas is generally more pleasing than those of hard boundaries; in addition, the visual distinctiveness of a hard boundary that persists over time would be mitigated. Furthermore, areas that are prone to edge windthrow would benefit from these softer boundaries.

It is unlikely that mapping of forest landscapes will change based on this study. GIS software is not yet capable of generating variable boundaries around polygons. Until this happens, any application of the results of this study will be stand-level and on the ground. New spatially explicit ecosystem models designed to encompass variable mortality will be able to simulate the impacts of this type of complexity on long term forest dynamics (see work on LLEMS by Seely et al., 2003).

5.5 Why Has This Not Been Studied Before?

One of the primary implications of this thesis is that 10% to 30% of landscapes such as the ones studied here in the Arrow Lakes Forest District might be in an intermediate forest condition *between polygons*. This is a non-trivial amount of forest area. There are several reasons why this may not have been examined earlier. First, the psychological need for classification of entities into discrete classes is paramount. In all fields and in all cultures, dichotomies and dualisms have been created where they only partially exist. Classification schemes for species, for soil types, for colour palettes and more explicitly exclude intermediates. Second, the results from this study may be an artifact of the particular disturbance events of 1993-1997 in the Arrow Lakes and might not be found elsewhere. This is an unavoidable limitation of sampling in ecology and it is difficult to directly test the impacts of this: the same study would need to be repeated in many more places and at many more time periods. Third, the sampling and statistical techniques

needed to describe such boundaries have not existed until the past several decades. The questions posed in this study could not be answered in Fischerian statistical modes of analysis because the data points are not independent. Spatial techniques were necessary to be able to answer these questions; without them, the questions may not have been asked.

Fourth, it is probable that the heterogeneity and differences found here at the boundaries of my study will change over time. Horizontal forces, such as wind, may either expand or narrow boundaries resulting in forest patches with hard boundaries. More likely, however, boundaries from old fires that were particularly broad would have been classified into their own forest cover polygons, and smaller ones would just be averaged into the neighbouring polygons.

A fifth possible reason for this oversight is that aerial photos or other remote sensing tools would perceive an overstory tree boundary at the junction of 100% mortality and the first live trees at the boundary (Edwards & Lowell 1996). The visual contrast between a live tree and 100% dead trees is remarkable; however, the ecosystem and understory regeneration would reflect different conditions in the boundary gradient.

I do not claim that *all* natural disturbance boundaries are soft. Indeed, two of the fire sites (F18 and F19) had very hard boundaries. The proportion of soft to hard boundaries will likely vary between regions and fires and along single fire boundaries. Though a casual set of observations may suggest hard boundaries, this does not imply that boundaries are necessarily hard; indeed, it is well known that objects that are not looked for will not be found.

5.6 Future Studies

Several possible research avenues lead directly from this current study. They will each be introduced briefly with references to literature and with links to the current study. All of these were originally proposed as part of this thesis, but were delayed for future studies as the magnitude of the research effort required was recognized.

5.6.1 Effect of Natural Disturbance Boundary Zone Variation On Wildlife Habitat Attributes

Forest stand structure, both living and dead, has become an important topic in wildlife habitat research (Swanson 1992; Bunnell 1995; Lindenmayer 1995; Lofroth 1998; Niemela 1999; Payer & Harrison 2000). Coarse woody debris (CWD) has been identified as important for a

diverse number of species—including invertebrates, salamanders, small and medium mammals (Maser & Trappe 1984; Lofroth 1998)—as well as playing a role in nutrient cycling, erosion control and other ecological processes (Maser & Trappe 1984; Harmon et al. 1986; Stone et al. 1998). These roles played by CWD vary over the long temporal scales that are required to complete the decomposition (Lofroth 1998). Snags, or standing dead or dying trees, also play important wildlife habitat roles (Backhouse 1993; Flanagan et al. 1998; Lofroth 1998; Chambers et al. 1999). Indeed, the importance of dead wood in various forms is generally well documented with many species-specific relationships now understood. What is less well documented and understood relates to the spatial patterns of these materials (Harmon et al. 1986) and to the incorporation of dead wood into management; how much should be left on site and where. The spatial relationships between intact forest and dead, disturbed forest may be important because of an individual organism's use of different seral stages and structural components for different functions (e.g., foraging, nesting, perching, shelter etc. (Bowman & Harris 1980)).

The potential influences of soft edge habitat, as contrasted with hard edges, for wildlife are largely unknown (Voller 1998). However, nest predation has been shown to be higher at hard edges (Ratti & Reese 1988; Suarez et al. 1997). Very little work has investigated soft edges in forest harvests because hard edges are almost exclusively created. One example where boundary cuts were made at the edges of clearcuts was inconclusive (Fleming & Giuliano 1998) but other evidence is beginning to suggest that soft edges in harvested areas have strikingly reduced predation rates (Fleming & Giuliano 2001). Past work examining local natural disturbance patterns as a basis for management has generally focused on landscape patterns or highly visible features such as wildfire islands (Schmoldt et al. 1999). With few exceptions, which are usually related to the creation of wind firmness, harvested edges are usually hard, with little attempt to emulate local naturally-produced edges.

Objectives for this additional study include examination of the edges of natural disturbance patches for their spatial characteristics, species composition and variability of features identified as important for wildlife habitat. These include snag abundances by size class, live tree retention, coarse woody debris, and vegetation/woody shrub abundances. The research questions would be: What are the structural features within boundary zones? Do they vary between disturbance types? Does the spatial gradient of tree mortality at the boundaries create a spatial gradient of structural features? Successional dynamics were shown to be non-linear across

the boundary. Are structural features also non-linear across the boundary? The primary goals of the study would be to establish baseline structural attributes of natural disturbances to which can be compared harvested blocks with respect to structural retention. The majority of this data is already collected for the sites used in my thesis.

5.6.2 Probabilistic Modeling

Preliminary understanding of a process or a set of processes should be incorporated into a conceptual model as a starting point for unifying related but separate parts of a system (Kimmins 1997). While conceptual models force us to elucidate our understanding of how process and patterns act and interact they can only build hypotheses; mathematical or computer based models must be used to test hypotheses or make predictions. Simulation models can be seen as the final stage of the pathway through scientific exploration: induction, deduction, and modeling. Alternatively, they are used as scientific tools to explain existing data and predict other aspects of nature (Hilborn & Mangel 1997). Models are a necessary step in synthesizing knowledge of processes, linking disparate reductionist experiments, and predicting future events, particularly as future conditions change.

The relationship between probabilistic models and process models involves a question of scale. Since every process is deterministic, all processes could, in theory, be modeled exactly if every feature of the process, and all the factors influencing it, can be understood and measured. In ecology, no process can be completely and successfully parameterized as there are too many antecedent determinants, each acting at different scales. As a result, traditional deterministic models are forced to choose the factors *a priori* that are deemed most important and that are believed to be the primary determinants of the process of interest. Thus, all deterministic models in ecology suffer from an incomplete set of parameters with a predefined set of rules that link the parameters. This results in the trade-off between more parameters--and thus better fit to the data--and fewer parameters--and thus better broad scale generality. An alternative approach is to scale-up the observations such that the original process of interest becomes probabilistic; observing any process at a higher spatial or temporal scale, it appears probabilistic.

In the present thesis, the influence of several antecedent determinants was measured as well as estimates of their probability of being influential in a given boundary. These variables included BA of susceptible trees, aspect, density and age. Every fire site examined here was also

affected by unmeasured, spatially trending data, and these should be identified and manipulated in the models. The mean and variance of boundary width in fires and MPB were also estimated and these values would be used in the process of model construction and simulation. A simple simulation model using all of these factors and probability measures could be constructed to generate simulations of natural disturbance boundaries. More and better data would result in better estimates of the probability parameters.

The primary objective of this future study would be to create a probabilistic stand scale spatial simulation model for natural disturbance boundaries. If this is tied to other GIS layers of stand attributes, stand variables could be estimated under no boundary conditions (hard edges) vs. complex boundary conditions.

5.6.3 Designed Sustainability: Incorporating Disturbance Boundaries into Management Scenarios

Forest management in British Columbia and the rest of Canada is engaged in a struggle to determine the sustainability of its current practices (Nguyen-Xuan et al. 2001; Delong 2001; Armstrong 2001; Cumming 2001b). Included in this is the Innovative Forest Practices Agreement (Arrow Forest Licensee Group 1999). The future study described here would link my research with collaborative work that is attempting to model future forest conditions based on current or planned forest management practices. This work will necessitate the incorporation of my data into a larger modeling framework capable of examining ecosystem processes; it will complement the numerous other natural disturbance based studies that have had as an explicit goal to model future management decisions on natural patterns and processes (D'Eon et al. 2000; Andison & Cumming 2001).

Literature cited

- Abrams, M.D. and Scott, M.L. 1989. Disturbance-mediated accelerated succession in two Michigan forest types. *For. Sci.* **35**: 42-49.
- Abrams, M.D., Sprugel, D.G., and Dickmann, D.I. 1985. Multiple successional pathways on recently disturbed jack pine sites in Michigan. *For. Ecol. Manag.* **10**: 31-48.
- Adamowicz, W.L. and Veeman, T.S. 1998. Forest policy and the environment - changing paradigms. *Canadian Public Policy* **24 (Suppl 2)**.
- Agee, J.K. 1993. *Fire ecology of Pacific Northwest forests*. Island Press, Washington D.C.
- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. *In* Second international symposium on information theory. *Edited by* B.N. Petrov and F. Csaki. Akademiai Kiado, Budapest. pp. 267-281.
- Akaike, H. 1987. Factor analysis and AIC. *Psychometrika* **52**: 317-332.
- Anderson, D.R. and Burnham, K.P. 2002. Avoiding pitfalls when using information-theoretic methods. *J. Wildl. Manag.* **66** : 912-918.
- Anderson, D.R., Burnham, K.P., and Thompson, W.L. 2000. Null hypothesis testing: Problems, prevalence, and an alternative. *J. Wildl. Manag.* **64**: 912-923.
- Anderson, D.R., Link, W.A., Johnson, D.H., and Burnham, K.P. 2001. Suggestions for presenting the results of data analyses. *J. Wildl. Manag.* **65**: 373-378.
- Andison, D.W. 2001. Quicknote 6. The "even aged" boreal forest myth. 6 Foothills Model Forest, Alberta, Canada.
- Andison, D.W. and Cumming, S.G. (eds.). 2001. *Natural disturbance & forest management: What's happening and where's it going*. Sponsored by: Foothills Model Forests and Sustainable Forest Management Network. Conference in Edmonton, Alta. March 5-7, 2001.
- Andison, D.W. and Marshall, P.L. 1999. Simulating the impact of landscape-level biodiversity guidelines: A case study. *For. Chron.* **75**: 655-665.
- Andrews, P. and Bevins, C.D. **BehavePlus** Fire Modeling System. [1.0.0]. 2002. Missoula, MT., USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Lab, Fire Behavior Research Work Unit.
- Arbuckle, J.L. AMOS 4.01 (Build 346). 1999. Chicago, IL, SmallWaters Corp.
- Armleder, H.M., Stevenson, S.K., and Walker, S.D. 1992. Estimating the abundance of arboreal forage lichens. B.C. Ministry of Forests, Victoria.
- Armstrong, G.W. 2001. The rate of natural disturbance: implications for forest management and sustainability. *In* Conference in Edmonton, Alta. March 5-7, 2001. *Natural disturbance & forest management: What's happening and where's it going*. Sponsored by: Foothills Model Forests and Sustainable Forest Management Network.
- Arrow Forest Licensee Group . Arrow Innovative Forest Practices Agreement: Forestry Plan. 1999. Nelson, B.C.

- Asselin, H., Fortin, M.-J., and Bergeron, Y. 2001. Spatial distribution of late-successional coniferous species regeneration following disturbance in southwestern Quebec boreal forest. *For. Ecol. Manag.* **140**: 29-37.
- Attiwill, P.M. 1994a. Ecological disturbance and the conservative management of eucalypt forests in Australia. *For. Ecol. Manag.* **63**: 301-346.
- Attiwill, P.M. 1994b. The disturbance of forest ecosystems: the ecological basis for conservative management. *For. Ecol. Manag.* **63**: 247-300.
- Backhouse, F. 1993. Wildlife tree management in British Columbia. Co-publication of BC Environment, Workers' Compensation Board, BC Forest Service and FRDA Victoria, B.C.
- Barbosa, P. and Schultz, J.C. (eds.) 1987. Insect outbreaks. Academic Press, Inc, San Diego, USA .
- Barton, N.H. and Hewitt, G.M. 1985. Analysis of hybrid zones. *Annu. Rev. Ecol. Syst.* **16**: 113-148.
- Bentler, P.M. 1990. Comparative fit indexes in structural equation systems. *Psychological bulletin* **107**: 238-246.
- Bergeron, Y. and Dansereau, P.R. 1993. Predicting the composition of Canadian southern boreal forest in different fire cycles. *J. Veg. Sci.* **4**: 827-832.
- Bergeron, Y., Engelmark, O., Harvey, B., Morin, H., and Sirois, L. 1998. Key issues in disturbance dynamics in boreal forests: introduction. *J. Veg. Sci.* **9**: 463-468.
- Bergeron, Y. and Harvey, B. 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. *For. Ecol. Manag.* **92**: 235-242.
- Bergeron, Y., Harvey, B., Leduc, A., and Gauthier, S. 1999a. Forest management guidelines based on natural disturbance dynamics: Stand- and forest-level considerations. *For. Chron.* **75**: 49-54.
- Bergeron, Y., Richard, P.J.H., Carcaillet, C., Gauthier, S., Flannigan, M., and Prairie, Y.T. 1999b. Variability in fire frequency and forest composition in Canada's southeastern boreal forest: A challenge for sustainable forest management. *Conserv. Ecol. (Online)* **2**.
- Bollen, K.A. 1989. Structural equations with latent variables. Wiley, New York.
- Bond, W.J. and Wilgen, B.W. 1996. Fire and plants. Chapman & Hall Ltd, London, UK.
- Bowman, G.B. and Harris, L.D. 1980. Effect of spatial heterogeneity on ground-nest depredation. *J. Wildl. Manag.* **44**: 806-813.
- Brown, J.K. and Smith, J.K. (eds.) 2001. Wildland fire in ecosystems: effects of fire on flora. USDA For. Serv. Gen. Tech. Rep. RMRS-GTR-42-vol. 2 U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- Browne, M.W. and Cudeck, R. 1993. Alternative ways of assessing model fit. *In* Testing structural equation models. *Edited by* K.A. Bollen and J.S. Long. Sage, Newbury Park, CA. pp. 445-455.
- Bunnell, F.L. 1995. Forest-dwelling vertebrate faunas and natural fire regimes in British Columbia: patterns and implications for conservation. *Conser. Biol.* **9**: 636-644.

- Burnham, K.P. and Anderson, D.R. 1998. Model selection and inference: a practical information-theoretic approach. Springer, New York, USA.
- Burnham, K.P. and Anderson, D.R. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* **28**: 111-119.
- Burns, R.M. and Honkala, B.H. (tech.coords.) 1990. Silvics of North America: 1. Conifers; 2. Hardwoods. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington DC.
- Byrne, B.M. 2001. Structural equation modeling with AMOS. Basic concepts, applications and programming. Lawrence Erlbaum Associates, Publishers, Mahwah, NJ.
- Cadenasso, M.L. and Pickett, S.T.A. 2000. Linking forest edge structure to edge function: mediation of herbivore damage. *J. Ecol.* **88**: 31-44.
- Cadenasso, M.L. and Pickett, S.T.A. 2001. Effect of edge structure on the flux of species into forest interiors. *Conser. Biol.* **15**: 91-97.
- Cadenasso, M.L., Traynor, M.M., and Pickett, S.T.A. 1997. Functional location of forest edges: gradients of multiple physical factors. *Can. J. For. Res.* **27**: 774-782.
- Cattellino, P.J., Noble, I.R., Slatyer, R.O., and Kessel, S.R. 1979. Predicting the multiple pathways of plant succession. *Environ. Manage.* **3**: 41-50.
- Chamberlain, T.C. 1890. The method of multiple working hypotheses. *Science* **15**: 92.
- Chambers, C.L., McComb, W.C., and Tappeiner, J.C. 1999. Breeding bird responses to three silvicultural treatments in the Oregon Coast range. *Ecol. Appl.* **9**: 171-185.
- Chen, J., Franklin, J.F., and Spies, T.A. 1992. Vegetation responses to edge environments in old-growth douglas-fir forests. *Ecol. Appl.* **2**: 387-396.
- Chesson, P.L. and Case, T.J. 1986. Overview: non-equilibrium community theories: Chance, variability, history and coexistence. *In* Community ecology. *Edited by* J. Diamond and T.J. Case. Harper and Row, New York. pp. 229-239.
- Christensen, N.L., Bartuska, A.M., Brown, J.H., Carpenter, S., D'Antonio, C.M., Francis, R., Franklin, J.F., MacMahon, J.A., Noss, R.F., Parsons, D.J., Peterson, C.H., Turner, M.G., and Woodmansee, R.G. 1996. The report of the Ecological Society of America Committee on the scientific basis for ecosystem management. *Ecol. Appl.* **6**: 665-691.
- Cissel, J.H., Swanson, F.J., Grant, G.E., Olson, D.H., Gregory, S.V., Garman, S.L., Ashkenas, L.R., Hunter, M.G., Kertis, J.A., Mayo, J.H., McSwain, M.D., Swetland, S.G., Swindle, K.A., and Wallin, D.O. 1998. A Landscape Plan Based on Historical Fire Regimes for a Managed Forest Ecosystem: the Augusta Creek Study. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-422 USDA. Pacific Northwest Research Station, Portland, Oregon.

- Cissel, J.H., Swanson, F.J., and Weisberg, P.J. 1999. Landscape management using historical fire regimes: Blue River, Oregon. *Ecol. Appl.* **9**: 1217-1231.
- Clark, J.S. 1991. Disturbance and population structure on the shifting mosaic landscape. *Ecology* **72**: 1119-1137.
- Clements, F.E. 1916. Plant succession. Carnegie Institution of Washington Publication 242.
- Connell, J.H. and Slatyer, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* **111**: 1119-1144.
- Cooper, W.S. 1923a. The recent ecological history of Glacier Bay, Alaska: II. The present vegetation cycle. *Ecology* **4**: 223-246.
- Cooper, W.S. 1923b. The recent ecological history of Glacier Bay, Alaska: III. Permanent quadrats at Glacier Bay: an initial report upon a long-period study. *Ecology* **4**: 355-365.
- Crane, M.F. and Fischer, W.C. 1986. Fire ecology of the forest habitat types of central Idaho. USDA For. Serv. Gen. Tech. Rep. INT-GTR-218 United States Department of Agriculture. Forest Service. Intermountain Research Station.
- Crawley, M.J. 1997a. Life history and environment. *In Plant ecology. Edited by M.J. Crawley.* 2nd edition ed. Blackwell Science, Oxford, UK. pp. 73-131.
- Crawley, M.J. 1997b. The structure of plant communities. *In Plant ecology. Edited by M.J. Crawley.* 2nd ed. Blackwell Science, Oxford, UK. pp. 475-531.
- Cumming, S.G. 2001a. Forest type and wildfire in the Alberta boreal mixedwood: What do fires burn? *Ecol. Appl.* **11**: 97-110.
- Cumming, S.G. 2001b. Spatial ecology of fire in the boreal mixedwood. *In Conference in Edmonton, Alta. March 5-7, 2001. Natural disturbance & forest management: What's happening and where's it going.* Sponsored by: Foothills Model Forests and Sustainable Forest Management Network.
- Cumming, S.G., Burton, P.J., and Klinkenberg, B. 1996. Boreal mixedwood forests may have no representative areas - some implications for reserve design. *Ecography* **19**: 162-180.
- D'Eon, R.G., Johnson, J.F., and Ferguson, E.A. (eds.). 2000. Ecosystem management of forested landscapes: directions and implementation. Proceedings of a conference held in Nelson, B.C., Canada, 26-28 October 1998.
- Darwin, C. 1860. The origin of species by means of natural selection; or, preservation of favored races in the struggle for life. 6th Edition ed. A.L. Burt, New York.
- de Blois, S., Domon, G., and Bouchard, A. 2001. Environmental, historical, and contextual determinants of vegetation cover: a landscape perspective. *Landsc. Ecol.* **16**: 421-436.
- De Santo, T.L. and Willson, M.F. 2001. Predator abundance and predation of artificial nests in natural and anthropogenic coniferous forest edges in southeast Alaska. *J. Field Ornithol.* **72**: 136-149.
- DeBano, L.F., Neary, D.G., and Ffolliott, P.F. 1998. Fire's Effects on Ecosystems. John Wiley & Sons, Inc., Toronto.

- Delong, C. 2001. Ecosystem management at low cost: using nature's template to best advantage. *In* Conference in Edmonton, Alta. March 5-7, 2001. Natural disturbance & forest management: What's happening and where's it going. Sponsored by: Foothills Model Forests and Sustainable Forest Management Network.
- Delong, S.C. and Tanner, D. 1996. Managing the pattern of forest harvest - lessons from wildfire. *Biodivers. Conserv.* **5**: 1191-1205.
- Drury, W.H. and Nisbet, I.C.T. 1973. Succession. *Arnold Arboretum Journal* **54**: 331-368.
- Duchesneau, R. PRESTO. [0.0]. 2003.
- Eberhart, K.E. and Woodard, P.M. 1987. Distribution of residual vegetation associated with large fires in Alberta. *Can. J. For. Res.* **17**: 1207-1212.
- Edmonds, R.L., Agee, J.K., and Gara, R.I. 2000. *Forest: Health and Protection*. 1st ed. McGraw-Hill, USA.
- Edwards, G. and Lowell, K.E. 1996. Modeling uncertainty in photointerpreted boundaries. *Photogrammetric Engineering and Remote Sensing* **62**: 337-391.
- Egler, F.E. 1951. A commentary on American plant ecology based on the textbooks of 1947-1949. *Ecology* **32**: 673-695.
- Egler, F.E. 1954. Vegetation science concepts. 1. Initial floristic composition--a factor in old-field vegetation development. *Vegetatio* **4**: 412-417.
- Environmental Systems Research Institute, I. ArcView GIS 3.2. 1999.
- Fagan, W.F., Cantrell, R.S., and Cosner, C. 1999. How habitat edges change species interactions. *Am. Nat.* **153**: 165-182.
- Farris, M.A. and Lechowicz, M.J. 1990. Functional interactions among traits that determine reproductive success in a native annual plant. *Ecology* **71**: 548-557.
- Fastie, C.L. 1995. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology* **76**: 1899-1916.
- Finney, M.A. 1999. Mechanistic modeling of landscape fire patterns. *In* Spatial modeling of forest landscape change. *Edited by* D.J. Mladenoff and W.L. Baker. 1st ed. Cambridge University Press, Cambridge. pp. 189-209.
- Fisher, R.A. 1926. *The design and analysis of experiments*. Oliver and Boyd, Edinburgh.
- Flanagan, P.T., Morgan, P., and Everett, R.L. 1998. Snag recruitment in subalpine forests. *Northwest Sci.* **72**: 303-309.
- Fleming, K.K. and Giuliano, W.M. 1998. Effect of border-edge cuts on birds at woodlot edges in southwestern Pennsylvania. *J. Wildl. Manag.* **62**: 1430-1437.
- Fleming, K.K. and Giuliano, W.M. 2001. Reduced predation of artificial nests in border-edge cuts on woodlots. *J. Wildl. Manag.* **65**: 351-355.
- Forman, R.T.T. 1995. *Land Mosaics*. Cambridge University Press, Cambridge.

- Fortin, M.-J. 1994. Edge-detection algorithms for 2-dimensional ecological data. *Ecology* **75**: 956-965.
- Fortin, M.-J. 1997. Effects of data types on vegetation boundary delineation. *Can. J. For. Res.* **27**: 1851-1858.
- Fortin, M.-J. 1999. Effects of sampling unit resolution on the estimation of spatial autocorrelation. *Ecoscience* **6**: 636-641.
- Fortin, M.-J. and Drapeau, P. 1995. Delineation of ecological boundaries - comparison of approaches and significance tests. *Oikos* **72**: 323-332.
- Fortin, M.-J. and Gurevitch, J. 1993. Mantel tests: spatial structure in field experiments . *In* Design and analysis of ecological experiments. *Edited by* S.M. Scheiner and J. Gurevitch. Chapman & Hall, New York.
- Fortin, M.-J., Olson, R.J., Ferson, S., Iverson, L., Hunsaker, C., Edwards, G., Levine, D., Buterà, K., and Klemas, V. 2000. Issues related to the detection of boundaries. *Landsc. Ecol.* **15**: 453-466.
- Fortin, M.-J. and Payette, S. 2002. How to test the significance of the relation between spatially autocorrelated data at the landscape scale: A case study using fire and forest maps. *Ecoscience* **9**: 213-218.
- Foster, D.R., Knight, D.H., and Franklin, J.F. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems* **1**: 497-510.
- Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., and Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manag.* **155**: 399-423.
- Frelich, L.E. 2002. Forest dynamics and disturbance regimes: Studies from temperate evergreen-deciduous forests. Cambridge University Press, Cambridge.
- Frelich, L.E. and Reich, P.B. 1999. Disturbance severity and threshold responses in the boreal forest. *Conserv. Ecol.* (Online) **2**.
- Galindo-Leal, C. and Bunnell, F.L. 1995. Ecosystem management: Implications and opportunities for a new paradigm. *For. Chron.* **71**: 601-606.
- Gates, J.E. and Gysel, L.W. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* **59**: 871-883.
- Gehlhausen, S.M., Schwartz, M.W., and Augspurger, C.K. 2000. Vegetation and microclimatic edge effects in two mixed- mesophytic forest fragments. *Plant Ecol.* **147**: 21-35.
- Geiger, R. 1965. The climate near the ground. Harvard University Press, Cambridge, Mass.
- Gilbert, B., Weber, A., and Kimmins, J.P. 2003. Multipathway model of succession on Northern Vancouver Island. *Can. J. For. Res.* (*In press*).
- Gleason, H.A. 1926. The individualistic concept of plant associations. *Bulletin of the Torrey Botanical Club* **53**: 7-26.

- Glenn-Lewin, D.C. and van der Maarel, E. 1992. Patterns and processes of vegetation dynamics. *In* Plant succession: theory and prediction. *Edited by* D.C. Glenn-Lewin, R.K. Peet, and T.T. Veblen. Chapman & Hall, London. pp. 11-59.
- Gordon, A.D. 1999. Classification. Monographs on statistics and applied probability, 82. 2nd ed. Chapman & Hall/CRC, London.
- Gosz, J.R. 1991. Fundamental ecological characteristics of landscape boundaries. *In* Ecotones: The role of landscape boundaries in the management and restoration of changing environments. *Edited by* M.M. Holland, P.G. Risser, and R.J. Naiman. Chapman & Hall, New York, USA. pp. 8-30.
- Gosz, J.R. 1993. Ecotone hierarchies. *Ecol. Appl.* **3**: 369-376.
- Grace, J.B. and Pugesek, B.H. 1998. On the use of path analysis and related procedures for the investigation of ecological problems. *Am. Nat.* **152**: 151-159.
- Graham, R.T., Harvey, A.E., Jain, T.B., and Tonn, J.R. 1999. The effects of thinning and similar stand treatments on fire behavior in Western forests. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-463 Pacific Northwest Research Station, Portland, OR.
- Greene, D.F. and Johnson, E.A. 1989. A model of wind dispersal of winged or plumed seeds. *Ecology* **70**: 339-347.
- Greene, D.F. and Johnson, E.A. 1994. Estimating the mean annual seed production of trees. *Ecology* **75**: 642-647.
- Greene, D.F. and Johnson, E.A. 1996. Wind dispersal of seeds from a forest into a clearing. *Ecology* **77**: 595-609.
- Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D.D., Morin, H., Charron, I., and Simard, M.J. 1999. A review of the regeneration dynamics of North American boreal forest tree species. *Can. J. For. Res.* **29**: 824-839.
- Haila, Y., Hanski, I.K., Niemela, J., Punttila, P., Raivio, S., and Tukia, H. 1994. Forestry and the boreal fauna: Matching management with natural forest dynamics. *Ann. Zool. Fenn.* **31**: 187-202.
- Hall, K.R. and Maruca, S.L. 2001. Mapping a forest mosaic - A comparison of vegetation and bird distributions using geographic boundary analysis. *Plant Ecol.* **156**: 105-120.
- Halpern, C.B. 1988. Early successional pathways and the resistance and resilience of forest communities. *Ecology* **69**: 1703-1715.
- Hansen, A.J. and di Castri, F. (eds.) 1992. Landscape boundaries. Consequences for biotic diversity and ecological flows. Springer-Verlag, New York.
- Hargrove, W.W. and Pickering, J. 1992. Pseudoreplication: a *sine qua non* for regional ecology. *Landsc. Ecol.* **6**: 251-258.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, D., Anderson, N.H., Cline, S.P., Aumen, N.F., Sedell, J.R., Lienkaemper, W., Cromack Jr, K., and Cummings, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* **5**: 133-302.

- Harper, K.A. and Macdonald, S.E. 2001. Structure and composition of riparian boreal forest: new methods for analyzing edge influence. *Ecology* **82**: 649-659.
- Hartley, M.J. and Hunter, M.L. 1998. A meta-analysis of forest cover, edge effects, and artificial nest predation rates. *Conser. Biol.* **12**: 465-469.
- He, H.S. and Mladenoff, D.J. 1999. Spatially explicit and stochastic simulation of forest-landscape fire disturbance and succession. *Ecology* **80**: 81-99.
- Herlin, I.S. 2001. Approaches to forest edges as dynamic structures and functional concepts. *Landscape Research* **26**: 27-43.
- Hilborn, R. and Mangel, M. 1997. *Ecological detective: Confronting models with data*. Princeton University Press, Princeton.
- Hilborn, R. and Stearns, S.C. 1982. On inference in ecology and evolutionary biology: the problem of multiple causes. *Acta Biotheor.* **31**: 145-164.
- Holland, M.M., Risser, P.G., and Naiman, R.J. (eds.) 1991. *Ecotones: The role of landscape boundaries in the management and restoration of changing environments*. Chapman & Hall, New York.
- Holling, C.S. 1981. Forest insects, forest fires, and resilience. *In* *Fires regimes and ecosystem properties*. Edited by H.A. Mooney, T.M. Bonnicksen, N.L. Christensen, J.E. Lotan, and W.A. Reiners. Proc. Conf. Gen. Tech. Rep. WO-26 ed. Washington DC. pp. 445-463.
- Honnay, O., Verheyen, K., and Hermy, M. 2002. Permeability of ancient forest edges for weedy plant species invasion. *For. Ecol. Manag.* **161**: 109-122.
- Hoogland, J.J. and Boomsma, A. 1998. Robustness studies in covariance structure modeling. An overview and a meta-analysis. *Sociological Methods and Research* **26**: 329-367.
- Horn, H.S. 1974. The ecology of secondary succession. *Annu. Rev. Ecol. Syst.* **5**: 25-37.
- Huggard, D.J. and Vyse, A. 2002. Edge effects in high-elevation forests at Sicamous creek. Extension Note 62 Ministry of Forests Science Program, British Columbia.
- Huisman, J. and Weissing, F.J. 2001. Fundamental Unpredictability in Multispecies Competition. *Am. Nat.* **157**: 488-494.
- Hunter, M.L.Jr. 1993. Natural fire regimes as spatial models for managing boreal forests. *Biol. Conserv.* **65**: 115-120.
- Huston, M. and Smith, T. 1987. Plant succession: life history and competition. *Am. Nat.* **130**: 168-198.
- Hutto, R.L. 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain conifer forests. *Conser. Biol.* **9**: 1041-1058.
- Jacquez, G.M., Maruca, S., and Fortin, M.-J. 2000. From fields to objects: A review of geographic boundary analysis. *Journal of Geographic Systems* **2**: 221-241.

- Johnson, E.A., Miyanishi, K., and Weir, J.M.H. 1998. Wildfires in the western Canadian boreal forest: landscape patterns and ecosystem management. *J. Veg. Sci.* **9**: 603-610.
- Johnston, C.A., Pastor, J., and Pinay, G. 1992. Quantitative methods for studying landscape boundaries. *In* Landscape boundaries: Consequences for biotic diversity and ecological flows. *Edited by* A.J. Hansen and F. di Castri. Springer Verlag, New York. pp. 107-128.
- Jordan, G.J. Space, time, and uncertainty: detecting and characterizing boundaries in forest fire disturbances. 2002. PhD thesis. School of Resource and Environmental Sciences. Simon Fraser University.
- Jørgensen, S.E. 1992. EXERGY AND ECOLOGY. *Ecol. Model.* **63**: 185-214.
- Jørgensen, S.E., Patten, B.C., and Straskraba, M. 1992. Ecosystems emerging - toward an ecology of complex-systems in a complex future. *Ecol. Model.* **62**: 1-27.
- Kay, J.J. 2000. Ecosystems as self-organizing holarchic open systems: Narratives and the second law of thermodynamics. *In* Handbook of ecosystem theories and management. *Edited by* S.E. Jørgensen and F. Müller. CRC Press-Lewis Publishers, pp. 135-160.
- Kay, J.J., Allen, T.F.H., Fraser, R., Luvall, J.C., and Ulanowicz, R. 2001. Can we use energy based indicators to characterize and measure the status of ecosystems, human, disturbed and natural? *In* Proceedings of the international workshop. Advances in energy studies: exploring supplies, constraints and strategies. Porto Venere, Italy. May 23-27 2000.
- Kent, M., Gill, W.J., Weaver, R.E., and Armitage, R.P. 1997. Landscape and plant community boundaries in biogeography. *Progress in Physical Geography* **21**: 315-353.
- Kimmins, J.P. 1997. Forest ecology: a foundation for sustainable management. 2nd ed. Prentice Hall, Upper Saddle River, NJ.
- Kingsolver, J.G. and Schemske, D.W. 1991. Path analyses of selection. *Trends Ecol. Evol.* **6**: 276-280.
- Kneeshaw, D.D. and Bergeron, Y. 1996. Ecological factors affecting the abundance of advance regeneration in Quebec's southwestern boreal forest. *Can. J. For. Res.* **26**: 888-898.
- Kohm, K.A. and Franklin, J.F. 1997. Creating a forestry for the 21st century: the science of ecosystem management. Island Press, Washington D.C., USA.
- Kremsater, L. and Bunnell, F.L. 1999. Edge effects: Theory, evidence and implications to management of western North American forests. *In* Forest fragmentation: Wildlife and management implications. *Edited by* J.A. Rochelle, L.A. Lehmann, and J. Wisniewski. Koninklijke Brill NV, Leiden, Netherlands. pp. 117-153.
- Krummel, J.R., Gardner, R.H., Sugihara, G., O'Neill, R.V., and Coleman, P.R. 1987. Landscape patterns in a disturbed environment. *Oikos* **48**: 321-324.
- Lakatos, I. 1978. The methodology of scientific research programmes. Cambridge University Press, Cambridge.
- Landres, P.B., Morgan, P., and Swanson, F.J. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecol. Appl.* **9**: 1179-1188.

- Laurance, W.F. and Yensen, E. 1991. Predicting the impacts of edge effects in fragmented habitats. *Biol. Conserv.* **55**: 77-92.
- Lavender, D.P., Parish, R., Johnson, C.M., Montgomery, G., Vyse, A., Willis, R.A., and Winston, D. (eds.) 1990. Regenerating British Columbia's forests. University of British Columbia Press, Vancouver.
- Leduc, A., Drapeau, P., Bergeron, Y., and Legendre, P. 1992. Study of spatial components of forest cover using partial Mantel tests and path analysis. *J. Veg. Sci.* **3**: 69-78.
- Legendre, P. 1986. Constrained clustering. *In* Developments in numerical ecology. *Edited by* P. Legendre and L. Legendre. Springer, New York. pp. 289-307.
- Legendre, P. and Fortin, M.-J. 1989. Spatial pattern and ecological analysis. *Vegetatio* **80**: 107-138.
- Lehmkuhl, J.F. and Ruggiero, L.F. Ruggiero, L.F., Aubrey, K.B., Carey, A.B., and Huff, M.H. 1991. Forest fragmentation in the Pacific Northwest and its potential effects on wildlife. USDA Forest Service PNW-GTR-285
- Leopold, A. 1933. Game management. Charles Scribner's Sons, New York.
- Leung, Y. 1987. On the impression of boundaries. *Geographical analysis* **19**: 125-151.
- Lewin, R. 1984. Why is development so illogical? *Science* **224**: 1327-1329.
- Lindenmayer, D.B. 1995. Forest disturbance, forest wildlife conservation and the conservative basis for forest management in the mountain ash forests of Victoria: Comment. *For. Ecol. Manag.* **74**: 223-231.
- Lloyd, K.M., McQueen, A.A.M., Lee, B.J., Wilson, R.C.B., Walker, S., and Wilson, J.B. 2000. Evidence on ecotone concepts from switch, environmental and anthropogenic ecotones. *J. Veg. Sci.* **11**: 903-910.
- Lofroth, E. 1998. The dead wood cycle. *In* Conservation biology principles for forested landscapes. *Edited by* J. Voller and S. Harrison. B.C. Ministry of Forests, Vancouver, B.C. pp. 185-214.
- Logan, J.A., White, P., Bentz, B.J., and Powell, J.A. 1998. Model analysis of spatial patterns in mountain pine beetle outbreaks. *Theor. Popul. Biol.* **53**: 236-255.
- Luck, G.W., Possingham, H.P., and Paton, D.C. 1999. Bird responses at inherent and induced edges in the Murray Mallee, South Australia. 2. Nest predation as an edge effect. *Emu* **99**: 170-175.
- Lundquist, J.E. 2000. A method of estimating direct and indirect effects of *Armillaria* root disease and other small-scale forest disturbances on canopy gap size. *For. Sci.* **46**: 356-362.
- MacDonald, E. and Coates, K.D. (eds.). 2002. 4th International workshop on disturbance dynamics in boreal forests. Disturbance processes and their ecological effects. August 9-14, Prince George, BC.
- Mailly, D., Kimmins, J.P., and Busing, R.T. 2000. Disturbance and succession in a coniferous forest of northwestern North America: simulations with DRYADES, spatial gap model. *Ecol. Model.* **127**: 183-205.
- Mardia, K.V. 1970. Measures of multivariate skewness and kurtosis with applications. *Biometrika* **57**: 519-530.
- Margalef, R. 1963. On certain unifying principles in ecology. *Am. Nat.* **97**: 357-374.

- Maser, C. and Trappe, J.M. (eds.) 1984. The seen and unseen world of the fallen tree. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-164 Pacific Northwest Research Station, Portland, Oregon.
- Matlack, G.R. 1993b. Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation* **66**: 185-194.
- Matlack, G.R. 1993a. Microenvironment variation within and among forest edge sites in the eastern United States. *Biol. Conserv.* **66**: 185-194.
- McCollin, D. 1998. Forest edges and habitat selection in birds: a functional approach. *Ecography* **21**: 247-260.
- McCullough, D.G., Werner, R.A., and Neumann, D. 1998. Fire and insects in northern and boreal forest ecosystems of North America. *Annu. Rev. Entomol.* **43**: 107-127.
- McIntire, E.J.B., Duchesneau, R., and Kimmins, J.P. 2001. The effects of natural disturbances on "succession": an ecosystem modelling approach. *In* Conference in Edmonton, Alta. March 5-7, 2001. Natural disturbance & forest management: What's happening and where's it going. Sponsored by: Foothills Model Forests and Sustainable Forest Management Network.
- McIntire, E.J.B. and Waterway, M.J. 2002. Clonal structure and hybrid susceptibility to a smut pathogen in microscale hybrid zones of northern wetland *Carex* (Cyperaceae). *Am. J. Bot.* **89**: 642-654.
- McQuillan, A.G. 2000. Using Fractal Geometry to Simulate the Distribution of Trees in Natural Stands.
- Meidinger, D. and Pojar, J. (eds.) 1991. Ecosystems of British Columbia. Research Branch. Ministry of Forests, B.C., Victoria, B.C.
- Meidinger, D., Trowbridge, R., Macadam, A., and Tolcamp, C. (eds.) 1998. Field manual for describing ecosystems in the field. Resources Inventory Branch, B.C. Ministry of Environment, Lands and Parks and Research Branch, B.C. Ministry of Forests, Victoria, B.C.
- Meiners, S.J. and Pickett, S.T.A. 1999. Changes in community and population responses across a forest- field gradient. *Ecography* **22**: 261-267.
- Ministry of Forests, B.C. and Ministry of Environment, B.C. 1995. Biodiversity Guidebook, Forest Practices Code. Forest Service, Victoria, B.C.
- Minnich, R.A. 1998. Vegetation, fire regimes, and forest dynamics. Springer-Verlag New York Inc, New York, USA. pp. 44-78.
- Mitchell, R.J. 1992. Testing evolutionary and ecological hypotheses using path analysis and structural equation modeling. *Funct. Ecol.* **6**: 123-129.
- Moore, M.M., Covington, W.W., and Fule, P.Z. 1999. Reference conditions and ecological restoration: A southwestern ponderosa pine perspective. *Ecol. Appl.* **9**: 1266-1277.
- Morgantini, L. 2001. From theory to practice: the implementation of the natural disturbance model in Weyerhaeuser Forest Management Areas in Alberta. *In* Conference in Edmonton, Alta. March 5-7, 2001. Natural disturbance

- & forest management: What's happening and where's it going. Sponsored by: Foothills Model Forests and Sustainable Forest Management Network.
- Muller, F., Windhorst, W., and Jørgensen, S.E. 1992. Recent problems in ecosystem theory -Conclusions of the workshop. *Ecol. Model.* **63**: 325-331.
- Murcia, C. 1995. Edge effects in fragmented forests - Implications for conservation. *Trends Ecol. Evol.* **10**: 58-62.
- Nguyen-Xuan, T., Bergeron, Y., and Leduc, A. 2001. Developing a forest management strategy based on natural disturbance dynamics for Northern Abitibi. *In* Conference in Edmonton, Alta. March 5-7, 2001. Natural disturbance & forest management: What's happening and where's it going. Sponsored by: Foothills Model Forests and Sustainable Forest Management Network.
- Niemela, J. 1999. Management in relation to disturbance in the boreal forest. *For. Ecol. Manag.* **115**: 127-134.
- Noble, I.R. and Slatyer, R.O. 1981. Concepts and models of succession in vascular plant communities subject to recurrent fire. *In* Fire and the Australian Biota. *Edited by* A.M. Gill, R.H. Groves, and I.R. Noble. Australian Academy of Science, Canberra. pp. 311-335.
- North, M., Chen, J., Smith, G., Krakowiak, L., and Franklin, J.F. 1996. Initial response of understory plant diversity and overstory tree diameter growth to a green tree retention harvest. *Northwest Sci.* **70**: 24-35.
- Oden, N.L., Sokal, R.R., Fortin, M.-J., and Goebel, H. 1993. Categorical wombling: detecting regions of significant change in spatially located categorical variables. *Geographical analysis* **25**: 336.
- Odum, E.P. 1969. The strategy of ecosystem development. *Science* **164**: 262-270.
- Pacific Forestry Centre . Forest health network archives pest data for British Columbia. Pacific Forestry Centre . 2001. Natural Resources Canada .
- Palik, B.J. and Murphy, P.G. 1990. Disturbance vs. edge effects in sugar-maple beech forest fragments. *For. Ecol. Manag.* **32**: 187-202.
- Parminter, J.V. 1998. Natural disturbance ecology. *In* Conservation biology principles for forested landscapes. *Edited by* J. Voller and S. Harrison. UBC Press, Vancouver, B.C. pp. 3-41.
- Parsons, D.J., Swetnam, T.W., and Christensen, N.L. 1999. Uses and limitations of historical variability concepts in managing ecosystems. *Ecol. Appl.* **9**: 1177-1178.
- Parsons, R., Morgan, P., and Landres, P. 2000. Applying the natural variability concept: towards desired future conditions. *In* Ecosystem management of forested landscapes: directions and implementation. Proceedings of a conference held in Nelson, B.C., Canada, 26-28 October 1998. *Edited by* R.G. D'Eon, J.F. Johnson, and E.A. Ferguson.
- Payer, D.C. and Harrison, D.J. 2000. Structural differences between forests regenerating following spruce budworm defoliations and clear-cut harvesting: implications for marten. *Can. J. For. Res.* **30**: 1965-1972.
- Perera, A.H., Buse, L.J., and Weber, M.G. (eds.) 2003. Emulating natural forest landscape disturbances: concepts and applications. Columbia University Press, New York, USA.

- Perry, D.A. 1988. Landscape pattern and forest pests. *Northwest Environmental Journal* **4**: 213-228.
- Peters, R.H. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge, UK.
- Peters, R.H. 1991. *A critique for ecology*. Cambridge University Press, Cambridge.
- Peterson, D.L. and Parker, V.T. (eds.) 1998. *Ecological scale: theory and applications*. Columbia University Press, New York.
- Petraitis, P.S., Dunham, A.E., and Niewiarowski, P.H. 1996. Inferring multiple causality: the limitations of path analysis. *Funct. Ecol.* **10**: 421-431.
- Pickett, S.T.A., Collins, S.L., and Armesto, J.J. 1987a. A herarchical consideration of causes and mechanisms of succession. *Vegetatio* **69**: 109-114.
- Pickett, S.T.A., Collins, S.L., and Armesto, J.J. 1987b. Models, mechanisms and pathways of succession. *Bot. Rev.* **53**: 335-371.
- Pickett, S.T.A. and White, P.S. (eds.) 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York.
- Platt, J.R. 1964. Strong inference . *Science* **146**: 347-353.
- Popper, K. 1979. *Objective knowledge*. Cambridge University Press, Cambridge.
- Protection Branch . British Columbia digital fire atlas. British Columbia Ministry of Forests . 2001.
- Pyne, S.J. 1995. *World fire--the culture of fire on Earth*. Henry Holt, New York.
- Ratti, J.T. and Reese, K.P. 1988. Preliminary test of the ecological trap hypothesis. *J. Wildl. Manag.* **52**: 484-491.
- Raynor, G.S. 1971. Wind and temperature structure in a coniferous forest and a contiguous field. *For. Sci.* **17**: 351-363.
- Redfearn, A. and Pimm, S.L. 1987. Insect outbreaks and community structure. *In* *Insect outbreaks. Edited by P. Barbosa and J.C. Schultz*. Academic Press, Inc, San Diego, USA. pp. 99-133.
- Reifsnyder, W.E. 1955. Wind profiles in a small isolated forest stand. *For. Sci.* **1**: 289-297.
- Rogers, P. 1996. *Disturbance ecology and forest management: a review of the literature*. USDA For. Serv. Gen. Tech. Rep. INT-GTR-336 USDA Forest Service, Intermountain Research Station.
- Rothermel, R.C. 1972. *A mathematical model for predicting fire spread in wildland fuels*. USDA For. Serv. Gen. Tech. Rep. INT-115 USDA Forest Service, Intermountain Forest and Range Experiment Station.
- Rusek, J. 1992. Distribution and dynamics of soil organisms across ecotones. *In* *Landscape boundaries: consequences for biotic diversity and ecological flows*. Springer-Verlag, New York, USA. pp. 196-214.
- Safranyik, L., Shore, T.L., Linton, D.A., and Rankin, L. 1999. *A population dynamics model for the mountain pine beetle, Dendroctonus ponderosae Hopk. (Coleoptera Scolytidae)*. Pacific Forestry Centre, Victoria, BC.

- Samman, S. and Logan, J. (eds.) 2000. Assessment and response to bark beetle outbreaks in the Rocky Mountain area. USDA For. Serv. Gen. Tech. Rep. RMRS-GTR-62 USDA, Forest Service, Rocky Mountain Research Station.
- Saracco, J.F. and Collazo, J.A. 1999. Predation on artificial nests along three edge types in a North Carolina bottomland hardwood forest. *Wilson Bull.* **111**: 541-549.
- SAS Institute Inc. SAS. [V. 8.1]. 2000. Cary, NC, USA.
- Saunders, S.C., Chen, J.Q., Drummer, T.D., and Crow, T.R. 1999. Modeling temperature gradients across edges over time in a managed landscape. *For. Ecol. Manag.* **117**: 17-31.
- Schemske, D.W. and Horvitz, C.C. 1988. Plant-animal interactions and fruit production in a neotropical herb: A path analysis. *Ecology* **49**: 1128-1137.
- Schmoldt, D.L., Peterson, D.L., Keane, R.E., Lenihan, J.M., McKenzie, D., Weise, D.R., and Sandberg, D.V. 1999. Assessing the effects of fire disturbance on ecosystems: a scientific agenda for research and management. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-455 U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.
- Schonewald, C.M. 2001. Introduction to boundary space: Contextual and disciplinary specifics. *Complexity* **6**: 41-57.
- Shipley, B. and Lechowicz, M.J. 2000. The functional co-ordination of leaf morphology, nitrogen concentration, and gas exchange in 40 wetland species. *Ecoscience* **7**: 183-194.
- Shipley, B. 2000. Cause and correlation in biology: A user's guide to path analysis, structural equations and causal inference. Cambridge University Press, Cambridge.
- Shugart, H.H. and West, D.C. 1980. Forest succession models. *BioScience* **30**: 308-313.
- Sit, V. and Taylor, B. (eds.) 1998. Statistical methods for adaptive management studies. Research Branch, B.C. Ministry of Forests, Victoria, B.C.
- Smith, F.A., Brown, J.H., and Valone, T.J. 1997. Path analysis: a critical evaluation using long-term experimental data. *Am. Nat.* **149**: 29-42.
- Smith, J.K. (eds.) 2000. Wildland fire in ecosystems: effects of fire on fauna. USDA For. Serv. Gen. Tech. Rep. RMRS-GTR-42 vol. 1 U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- Smith, T. and Huston, M. 1989. A theory of the spatial and temporal dynamics of plant communities. *Vegetatio* **83**: 49-69.
- Spence, J.R. and Volney, W.J.A. 1999. EMEND: ecosystem management emulating natural disturbance. 1999-14 Sustainable Forest Management Network, Alberta, Canada.
- Sprugel, D.G. 1991. Disturbance, equilibrium, and environmental variability: what is 'natural' vegetation in a changing environment. *Biol. Conserv.* **58**: 1-18.

- Steele, R. 1994. The role of succession in forest health. *Journal of Sustainable Forestry* 2: 183-190.
- Steinberg, E.K. and Kareiva, P. 1997. Challenges and opportunities for empirical evaluation of "spatial theory". *In* Spatial ecology: The role of space in population dynamics and interspecific interactions. *Edited by* D. Tilman and P. Kareiva. Princeton University Press, Princeton, NJ. pp. 318-332.
- Stephenson, N.L. 1999. Reference conditions for giant sequoia forest restoration: Structure, process, and precision. *Ecol. Appl.* 9: 1253-1265.
- Stepnisky, D. and Schmiegelow, F. 2001. Salvage logging: does removal of post-fire timber result in the loss of a cavity nesting bird community? *In* Conference in Edmonton, Alta. March 5-7, 2001. Natural disturbance & forest management: What's happening and where's it going. Sponsored by: Foothills Model Forests and Sustainable Forest Management Network.
- Stevenson, J.D., Mackenzie, K.L., and Mahon, T.E. 1998. Response of small mammals and birds to partial cutting and clearcutting in northwest British Columbia. *For. Chron.* 74: 703-713.
- Stone, J.N., MacKinnon, A., Parminter, J.V., and Lertzman, K.P. 1998. Coarse woody debris decomposition documented over 65 years on southern Vancouver Island. *Can. J. For. Res.* 28: 788-793.
- Stuart, J.D. 1984. Hazard rating of lodgepole pine stands to mountain pine beetle outbreaks in southcentral Oregon. *Can. J. For. Res.* 14: 666-671.
- Sturtevant, B.R., Bissonette, J.A., and Long, J.N. 1996. Temporal and spatial dynamics of boreal forest structure in western Newfoundland: silvicultural implications for marten habitat management. *For. Ecol. Manag.* 87: 13-25.
- Suarez, A.V., Pfennig, K.S., and Robinson, S.K. 1997. Nesting success of a disturbance-dependent songbird on different kinds of edges. *Conser. Biol.* 11: 928-935.
- Sullivan, T.P., Lautenschlager, R.A., and Wagner, R.G. 1999. Clearcutting and burning of northern spruce-fir forests: implications for small mammal communities. *J. Appl. Ecol.* 36: 327-344.
- Swanson, F.J.F. 1992. New forestry principles from ecosystem analysis of pacific northwest forests. *Ecol. Appl.* 2: 262-274.
- Swetnam, T.W., Allen, C.D., and Betancourt, J.L. 1999. Applied historical ecology: Using the past to manage for the future. *Ecol. Appl.* 9: 1189-1206.
- Tansley, A.G. 1920. The classification of vegetation and the concept of development. *J. Ecol.* 8: 118-149.
- ter Braak, C.J.F. and Smilauer, P. Canoco for Windows. Ver. 4.02. 1999. Wageningen, The Netherlands, Centre for Biometry Wageningen, CPRO-DLO.
- TerraSeer . BoundarySeer. [V1.0]. 2001.
- Thoreau, H.D. 1860. The succession of forest trees. Reprinted in 1893 in *Excursions*. Houghtin, Mifflin & Co., Boston.
- Tilman, D. 1985. The resource-ratio hypothesis of plant succession. *Am. Nat.* 125: 827-852.

- Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecol. Monogr.* **57**: 189-214.
- Turner, M.G. 1989. Landscape ecology: the effect of pattern on process. *Annu. Rev. Ecol. Syst.* **20**: 171-197.
- Turner, M.G. and Bratton, S.P. 1987. Fire, grazing, and the landscape heterogeneity of a Georgia barrier island. *In* Landscape heterogeneity and disturbance. *Edited by* M.G. Turner. Springer-Verlag, New York. pp. 85-101.
- Turner, M.G., Gardner, R.H., Dale, V.H., and O'Neill, R.V. 1989. Predicting the spread of disturbance across heterogeneous landscapes. *Oikos* **55**: 121-129.
- Turner, M.G., Gardner, R.H., and O'Neill, R.V. 2001. Landscape ecology in theory and practice: Pattern and process. Springer-Verlag, New York, USA.
- Turner, M.G., Hargrove, W.W., Gardner, R.H., and Romme, W.H. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *J. Veg. Sci.* **5**: 731-742.
- Turner, M.G., Romme, W.H., Gardner, R.H., O'Neill, R.V., and Kratz, T.K. 1993. A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes. *Landsc. Ecol.* **8**: 213-227.
- Ulanowicz, R. 1997. Ecology, the ascendent perspective. Columbia University Press, New York.
- Voller, J. 1998. Managing for edge effects. *In* Conservation biology principles for forested landscapes. *Edited by* J. Voller and S. Harrison. UBC Press, Vancouver, B.C. pp. 215-234.
- Whelan, R. 1995. The ecology of Fire. Cambridge University Press, Cambridge.
- White, P.S. and Pickett, S.T.A. 1985. Natural disturbance and patch dynamics: an introduction. *In* The ecology of natural disturbance and patch dynamics. *Edited by* S.T.A. Pickett and P.S. White. Academic Press, Inc., Orlando, USA. pp. 3-9.
- Whittaker, R.H. 1953. A consideration of climax theory: the climax as a population and pattern. *Ecol. Monogr.* **23**: 41-78.
- Wiens, J.A. 1989. Spatial scaling in ecology. *Funct. Ecol.* **3**: 385-397.
- Wiens, J.A., Crawford, C.S., and Gosz, J.R. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* **45**: 421-427.
- Womble, W.H. 1951. Differential systematics. *Science* **114**: 315-322.
- Wootton, J.T. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology* **75**: 151-165.
- Wright, S. 1921. Correlation and causation. *J. Agric. Res.* **10**: 557-585.
- Yahner, R.H. 1988. Changes in wildlife communities near edges. *Conser. Biol.* **2**: 333-339.
- Zmyslony, J. and Gagnon, D. 2000. Path analysis of spatial predictors of front-yard landscape in an anthropogenic environment. *Landsc. Ecol.* **15**: 357-371.
- Zucchini, W. 2000. An introduction to model selection. *Journal of Mathematical Psychology* **44**: 41-61.