POST-FIRE TREE ESTABLISHMENT PATTERNS AT THE SUBALPINE FOREST-ALPINE TUNDRA ECOTONE: A CASE STUDY IN MOUNT RAINIER NATIONAL PARK

A Dissertation

by

KIRK M. STUEVE

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August 2009

Major Subject: Geography

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Approved by:

Chair of Committee,	Andrew C. Millington
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ABSTRACT

Post-fire Tree Establishment Patterns at the Subalpine Forest-Alpine Tundra Ecotone: A Case Study in Mount Rainier National Park. (August 2009)

Kirk M. Stueve, B.A., Minnesota State University Moorhead;
M.A., University of Southern California
Chair of Advisory Committee: Dr. Andrew C. Millington

Climatic changes have induced striking altitudinal and latitudinal vegetation shifts throughout history. These shifts will almost certainly recur in the future; threatening other flora and fauna, and influencing climate feedback loops. Changes in the spatial distribution of vegetation are most conspicuous at physiognomically distinct ecotones, particularly between the subalpine forest and alpine tundra. Traditionally, ecological research has linked abiotic variables with the position of this ecotone (e.g., cold temperatures inhibit tree survival at high elevations). Thus, the prevailing assumption states that this ecotone is in equilibrium or quasi-equilibrium with the surrounding physical environment and that any dynamic shifts express direct linkages with the physical environment.

This dissertation employs a landscape ecology approach to examine the abiotic and biotic ecological mechanisms most important in controlling tree establishment at this ecotone. The study site is on the western slopes of Mount Rainier, which was severely burned by a slash fire in 1930. Therefore, a crucial underlying assumption is that the ecological mechanisms controlling tree establishment are similar at disturbed and undisturbed sites. I exploited the use of 1970 CORONA satellite imagery and 2003 aerial photography to map 33 years of changes in arboreal vegetation. I created detailed maps of abiotic variables from a LIDAR-based DEM and biotic variables from classified remotely sensed data. I linked tree establishment patterns with abiotic and biotic variables in a GIS, and analyzed the correlations with standard logistic regression and logistic regression in the hierarchical partitioning framework at multiple spatial resolutions.

A biotic factor (proximity to previously existing trees) was found to exert a strong influence on tree establishment patterns; equaling and in most cases exceeding the significance of the abiotic factors. The abiotic setting was more important at restricted spatial extents near the extreme upper limits of the ecotone and when analyzing coarse resolution data, but even in these cases proximity to existing trees remained significant. The strong overall influence of proximity to existing trees on patterns of tree establishment is unequivocal. If the underlying assumption of this dissertation is true, it challenges the long-held ecological assumption that vegetation in mountainous terrain is in equilibrium with and most strongly influenced by the surrounding physical environment.

DEDICATION

To my wife (Mary) and two sons (Caden and Carter)

ACKNOWLEDGEMENTS

The primary academic advisor plays a pivotal role in any Ph.D. program in terms of mentoring and ensuring the timely completion of the dissertation. Dr. Andrew C. Millington fulfilled this role superbly by offering exceptional leadership, patience, timely critical reviews, support, candor, and advice in successfully guiding me through the completion of my dissertation. He ambitiously embraced the responsibility and challenge of advising me despite having arrived at the geography department from England nearly two years after the commencement of my PhD program. His exceptional influence will serve me well throughout my career. I am also extremely grateful to all of my advisory committee members for supporting my research endeavors and enhancing my professional development. In particular, Dr. Lafon demonstrated great guidance, patience, and care in assisting me with the publication of my first academic paper in *Area*. Dr. Popescu provided contagious enthusiasm for research and remote sensing that inspired me to explore remote sensing applications in biogeography and ecology. He also selflessly responded to my requests for fellowship reference letters at a moment's notice. Dr. Klein continually offered technically sound suggestions and support for my research. I would not be in this position without their steadfast support and encouragement.

I am very appreciative of Dr. Liu for providing exceptional training in quantitative analysis and remote sensing. His enthusiasm for teaching and superior work ethic is unrivaled. He also instilled a technical philosophy in me that is indispensable in

my research. That is, if you do not know how to do something, go figure it out on your own by reading the help section, researching an online discussion forum, and/or performing trial and error. If that fails, repeat the steps and try again until you succeed.

I thank Dr. Cairns for inspiring my interests in ecotones and providing advanced quantitative training in his plant geography course. The combination of substantive biogeographic/ecological discussions and detailed labs throughout his course were instrumental in honing my critical thinking skills and improving my ability to pose good research questions within the context of the literature. He also provided helpful comments throughout the formative stages of my dissertation.

I am grateful to Dr. Sherman for offering generous funding opportunities, and exploiting his leadership position to channel the skills of a talented faculty and elevate the national status of the geography department to unprecedented heights. It was a privilege to experience this dramatic transition during my tenure at the department.

I thoroughly enjoyed the comradery of the students in the geography department and I thank all of my classmates (past and present) for their friendship and support. I am especially grateful to Rachel Isaacs for helping me to complete my field research at Mount Rainier and offering encouragement throughout the completion of my dissertation. I also owe her a debt of gratitude for helping me to format and revise this dissertation. I do not know how I will be able to repay her, but I think a funded trip to Denali is a good start. I am particularly thankful for the friendship and support of Dr. Zengwang Xu, Matthew Clemonds, Michelle Simms, Sandra Metoyer, Lei Meng, Serena Aldrich, William Flatley, Daehyun Kim, Eugene Farrell, Adriana Martinez, and

Wansang Ryu. I also thank all other family and friends that supported me throughout this process, especially my mother.

About four years ago, I was exploring the possibility of selecting some treeline sites near Mount Rainier for my dissertation research. I sent a simple e-mail to Dr. Rochefort inquiring about a paper that she had published on tree establishment in subalpine parkland communities surrounding Mount Rainier, and received a supportive response. That simple e-mail morphed into a flurry of additional e-mails, conference calls, and a personally rewarding collaboration that included Dr. Cerney and Ms. Kurth. I am forever grateful to all three women for investing their time and mental energy with an unknown PhD student from Texas. Their support, encouragement, and critical reviews were crucial components in developing my dissertation topic and ultimately publishing Chapter V in the *Journal of Vegetation Science*.

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CHAPTER I

INTRODUCTION

Vegetation is dynamic and constantly changing, responding to its surrounding abiotic and biotic environment at multiple temporal and spatial scales. Indeed, striking altitudinal and latitudinal shifts in vegetation have been found to occur throughout the past during periods of climatic warming and cooling. The beginning stages of these shifts are most obvious at ecotones, particularly in mountainous landscapes where the distinct altitudinal zonation of vegetation creates sharp boundaries between subalpine forest and alpine tundra (von Humboldt 1807; Troll 1973b). Within the last 10,000 years, this ecotone has been anywhere from 5-400 m higher throughout much of the northern hemisphere (Lloyd &Graumlich 1997; Pisaric et al. 2003; Kullman &Kjällgren 2006) and it will probably shift again in the future. These shifts may exert pressure on existing flora and fauna, potentially serve as an indicator of climate change, and influence climate feedback loops (Körner 1998; Renssen et al. 2005).

My aim is to use remote sensing and GIS techniques, within a landscape ecology framework, to explain spatial patterns of arboreal vegetation at the subalpine forest-alpine tundra ecotone in Mount Rainier National Park. I also consider spatial scale, statistical techniques, and hierarchical ecological processes in explaining these patterns. In doing so, I address research questions pertinent to both treeline ecology and landscape

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This dissertation follows the style of *Journal of Vegetation Science.*

ecology. The majority of past studies have been conducted at fine spatial scales with exhaustive fieldwork, or at broad spatial scales with restricted data sets (e.g., 30-m USGS DEM and aerial photography). Here, I utilize the broader perspective of a geographer to bridge the divide between the fine- and broad-scale studies in order to improve explanations of tree establishment at this ecotone.

1.1 Ecotones

Frederick Clements first developed the ecotone concept in 1897 and Burton Livingston refers to it several years later in 1903. Shortly thereafter, Clements (1905) described the ecotone to be a stress line or tension zone connecting points of change between disparate ecological communities. By 1933, Aldo Leopold had identified unique species-response curves at ecotones and proclaimed this phenomenon to be the edge effect. Eugene Odum (1959) described ecotones as tension belts between two or more diverse communities where the number and density of species is often greater than the surrounding area. Ecological transition zones continued to garner attention from prominent ecologists throughout the remainder of the twentieth century (Harris 1988) and persist as a topic of paramount ecological importance to the present day (Beckage et al. 2008).

The primary impetus for much of the past research concerning ecotones relied on the supposition that useful ecological insights might be gained from studying pattern and process at the periphery of adjacent ecological communities (Walker et al. 2003). That is to say, distinct physiognomic differences between plant communities at ecotones facilitate the ability of biogeographers and ecologists to observe and analyze ecological interactions. The aforementioned rationale is the primary catalyst for the research addressed in this dissertation.

1.1.1 Terminology and dominant paradigms

Ecological definitions are inevitably controversial topics subject to influences from prevailing conceptual models for specific periods of time and ecotones are no exception. With his organismic view of vegetation, Clements (1905) clearly interpreted ecotones to be rather simple and abrupt boundaries demarcating different communities of large-scale vegetative units. Boundaries between different biomes often exhibit higher species composition (compared to the neighboring biomes) because they contain species from both neighboring plant communities (Odum 1971); providing a classic example of Clements' perspective. It should be noted that he also recognized the potential of the underlying influence of physical gradients and may, or may not, have appreciated the existence of ecotones across multiple scales (Yarrow & Marin 2007). Conversely, other ecologists philosophically aligned with Henry Gleason's (1926) individualistic concept of vegetation rejected Clement's conceptualization of ecotones. Many of these scholars championed more of an appreciation for the varied distribution of species along environmental gradients, which seemed especially pronounced at ecotones (e.g., Whittaker 1956). Some even boldly proclaimed transitional areas exhibiting rapid and large-scale shifts in community types to be ecoclines (Yarrow & Marin 2007).

Mountainous regions with varying slope angles, slope aspects, and particularly elevations often produced these so-called ecoclines (Jenik 1992). In the mid-twentieth century, Carl Troll (1939) successfully highlighted the ecological and scientific importance of this altitudinal zonation and he originally suggested that the environmental lapse rate (e.g., temperature decrease with increasing elevation) is largely responsible for generating different belts of vegetation in mountains. Later, Troll (1973a; 1973b) was drawn to the transitional area between the subalpine forest and alpine tundra; where he carried on a Gleasonian appreciation for the influences other environmental factors (e.g., topographic variability and snowpack) have in dictating patterns at ecoclines.

A broader perspective of ecotones began to emerge in the 1980's and 1990's when landscape ecology coalesced into a solid body of theory and applications (Forman 1995). Landscape ecology offered more of an appreciation of spatial scale and produced the key conceptual model of the patch-corridor-matrix (Forman 1995). This conceptual framework is largely considerate of both the Clementsian and Gleasonian interpretations of ecotones, depending upon the spatial scale of analysis. For example, an ecotone may appear very abrupt when considering a mapped spatial extent of several million hectares (e.g., similar to the view of Clements), but patterns of fine-scale patches influenced by steep environmental gradients begin to surface at smaller spatial extents of several thousand hectares or less (e.g., similar to the view of Gleason).

This dissertation employs the use of a landscape ecology perspective. At a broad spatial scale, I use Clements' theory to conceptualize and define the spatial extent of the study site in somewhat simplistic terms (e.g., for broadly identifying the boundary separating two distinct ecological communities). Conversely, Gleason's individualistic theory is the underlying foundation behind much of the analysis, which considers both fine and coarse spatial resolutions across a large spatial extent. Here, the focus remains on how spatially heterogeneous abiotic and biotic local site conditions influence the physiognomic structure of the ecotone.

1.1.2 Scientific importance

Historically, ecotones have been largely viewed from the two opposing perspectives: (1) a recurring problem or hindrance in defining the outer limits of particular ecological communities and in conducting objective research (e.g., plots must be carefully selected to avoid the likelihood of fluctuating species composition near ecotones); (2) unique ecological units worthy of being studied independently from traditional communities (Yarrow & Marin 2007). Since Clements first described the ecotone concept (1897), many ecologists have followed the former perspective (e.g., Watt & Jones 1948; Gedalof, & Smith 2001; Cripps & Eddington 2005), though some scholars have focused their research efforts on the latter (e.g., Lauer & Klaus 1975; Churkina & Svirezhev 1995; Hattenschwiler & Smith 1999; Oksanen & Minchin 2002) (Kark & van Rensburg 2006). In some extreme instances, several ecologists that published their work in the preeminent journal *Ecology* (e.g., Driscoll 1964; Allan et al. 1973) recommended intentionally avoiding ecotones altogether when conducting research in order to eliminate potential confusion when interpreting and extrapolating the results (Yarrow & Marin 2007). Consequently, ecotones (as opposed to relatively homogenous plant communities) have received considerably less attention from ecologists over the last 100 years than would have otherwise been possible.

Nevertheless, ecotones began to receive increased attention from both geographers and ecologists by the end of the twentieth century and beginning of the twenty first century (e.g., Kulllman 1997; Malanson 1997; MacDonald et al. 1998; Cairns 2001; Smith et al. 2003; Cairns 2004; Brodersen et al. 2006; Dutoit et al. 2007); especially in terms of climate change (Walther 2003), ideal places to explain how one functional group supplants another (Stueve et al. 2009), biodiversity hotspots that warrant careful consideration (Yarrow & Marin 2007), and suitable locations to otherwise test ecological theory (e.g., explain biodiversity, species coexistence, etc) (Wilson & Agnew 1992). At present, it has been suggested that additional research is required to satisfactorily explain how ecotones change over space and time, particularly at the subalpine forest-alpine tundra boundary (Holtmeier & Broll 2005).

1.1.3 Subalpine forest-alpine tundra ecotone

The subalpine forest-alpine tundra ecotone (treeline) is a unique transitional area separating closed-canopy forests and open alpine tundra in mountainous regions

(Hansen-Bristow et al. 1988). In general, this boundary occupies widely variable altitudes in all of the continents, except Antarctica (Figure 1-1), and exhibits an inverse relationship with latitude (Körner 1998) (Figure 1-2). In terms of the latter, there are noteworthy exceptions of tropical areas in the northern hemisphere and areas with humid temperate climates near oceans. In the tropics, abundant precipitation and cloud cover apparently causes the boundary to be slightly depressed compared to neighboring subtropical locations (Körner 1998). In humid temperate climates, heavy precipitation (particularly snow) probably depressed this boundary below what would be expected with latitudinal trends (Malanson et al. 2007). Local treeline elevations also have a tendency to deviate from these broad global trends (Holtmeier & Broll 2005).

Treeline has received considerable attention from scholars across the globe since the early twentieth century; posited to be primarily controlled by temperature and exist in equilibrium or quasi-equilibrium with the surrounding physical environment (e.g., Zotov 1938; Daubenmire 1954; Brown 1994b) (Table 1-1). The traditional hypothesis suggests cold temperatures and shortened growing seasons at high elevations hinder the survival of arboreal vegetation and favor the development of meadows (e.g., equilibrium with elevation) (Körner 1998). More recently, the treeline has been widely studied in terms of being a potential monitoring zone for the effects of climate change on vegetation (e.g., Noble 1993; Kupfer & Cairns 1996; Camarero & Gutierrez 2004; Walther 2003). However, some scholars remain cautious and suggest that the overriding

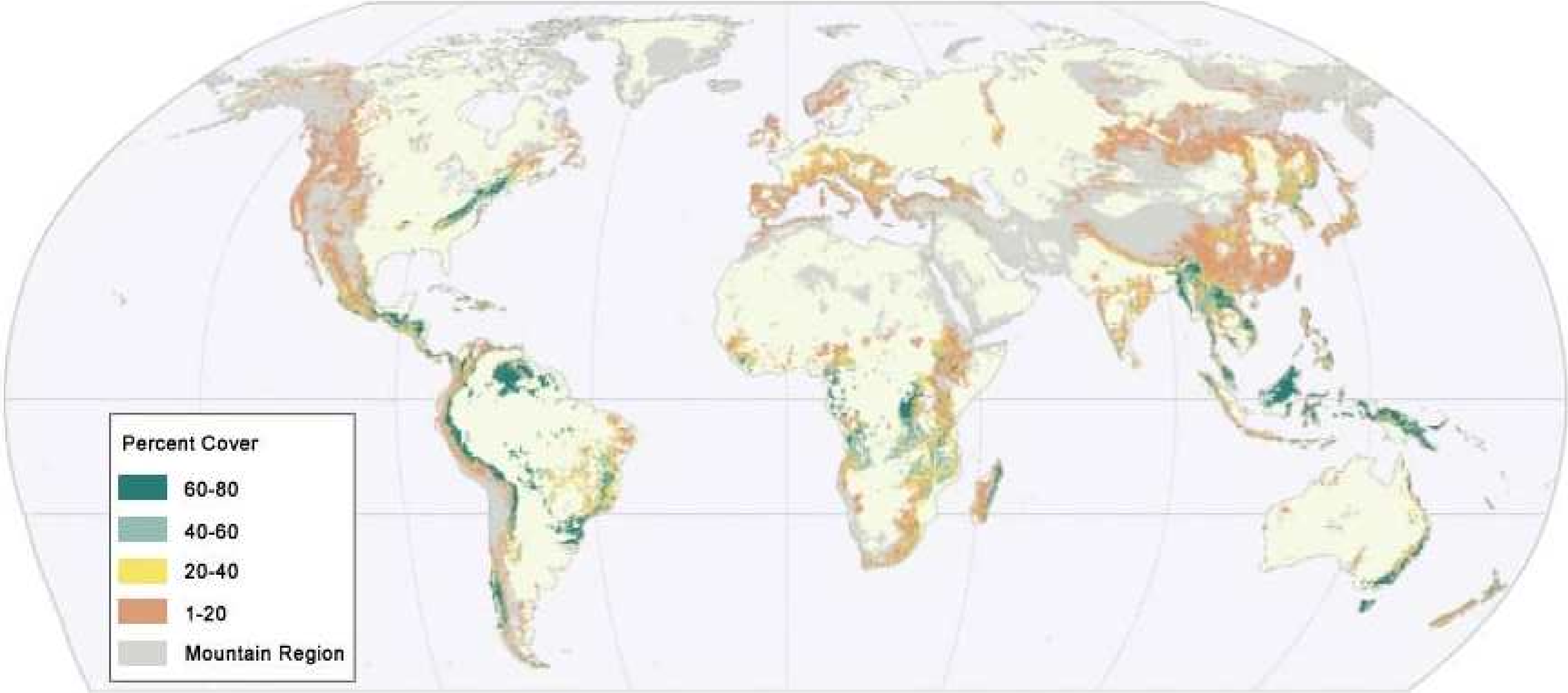


Figure 1-1: Global perspective of tree cover in mountainous regions (Source: map produced by United Nations Environment Programme, cited in *Mountain Watch Report* 2002).

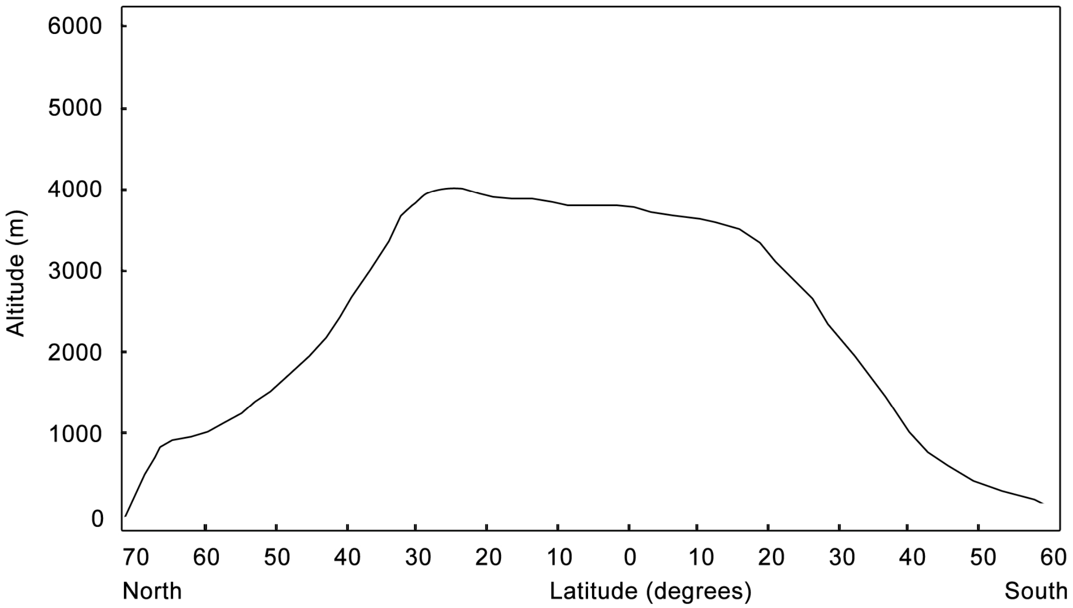


Figure 1-2: A graph modeled after figure 1 in Körner's 1998 paper. The solid line depicts treeline elevations at various latitudes.

influence of local site conditions and variable responses of different species to temperature fluctuations may produce complex nonlinear relationships between treeline elevations and climate change (Holtmeier & Broll 2005; Malanson et al. 2007). Assumptions of equilibrium with the surrounding physical environment still prevail, albeit with the addition of other topographic variables such as slope aspect and slope angle (e.g., Brown 1994b). If the treeline is to be used for monitoring climate change, additional research is necessary to explain the influence of local site conditions and synthesize a better climatic context (Holtmeier & Broll 2005).

Because the physiognomic characteristics of the treeline are widely variable at regional and local scales, defining the uppermost and lowermost borders of this boundary or an exact 'line' has been difficult and has often resulted in conflicting descriptions (Holtmeier 2003). A leading authority in this area (Holtmeier 2003) has classified the various descriptions of this boundary into four broad types: (1) an abrupt closed forest limit directly adjacent to alpine tundra; (2) a transitional zone spanning closed forest, patchy forest, and alpine tundra; (3) a transitional zone spanning closed forest, krummholz (a German term for short, crooked trees), and alpine tundra; and (4) a gradual transition across closed forest, stunted and/or crooked trees of the same species (also known as krummholz), and alpine tundra. Orographic (e.g., steep rock walls, talus cones, avalanche chutes, and slope debris), anthropogenic (e.g., timber, harvesting, grazing, etc), and other disturbance related influences may also produce uniquely shaped treeline boundaries that are depressed below their potential elevation limits and don’t fit well into Holtmeier’s classifications (Vale 1987; Butler et al. 2007).

To complicate matters further, a multitude of conflicting nomenclature such as the alpine treeline ecotone, timberline, treeline, forest line, tree limit, upper tree limit, and subalpine parkland have been used to describe the many different types of subalpine forest-alpine tundra boundaries that exist across the globe (Kullman 1993; Körner 1998; Germino et al. 2002). No consistent definition exists. Thus, in order to avoid more confusion, explicit definitions are necessary when making contributions to the peer-reviewed literature (Körner 1998).

For the purposes of this dissertation, the subalpine forest-alpine tundra transition zone is referred to as treeline and/or the subalpine parkland, and liberally defined as the area encompassed by two limiting boundaries. The lower boundary is the uppermost

Table 1-1: Published research conducted at the boundary between the subalpine forest and alpine tundra along with approximate corresponding altitudes. Use the listed altitudes with caution because of numerous conflicting treeline definitions used by ecologists. The list is not comprehensive but, rather, captures a snapshot of the breadth and history of treeline studies or observations. * indicates sites that were clearly influenced by disturbance and NA indicates that no treeline elevation was reported.

Country	Location	~Treeline Altitude (m)	Year	Author(s)
Australia	Snowy Mountains	2040	1976	Slatyer
Australia	Snowy Mountains	1780-1840	1993	Egerton & Wilson
Australia	Snowy Mountains	1830	1993	Wilson
Austria	Blaseneck Mountain	1800	1999	Gindl
Austria	Northern Calcareous Alps	1750-1900	2003a	Dullinger, Dirnböck, & Grabherr
Austria	Mount Patscherkofel	2180	2004	Oberhuber
Canada	Rocky Mountains (Mount Forbes)	2100	1899	Wilcox
Canada	Canadian Rockies (Mount Kitchi)	1798	1915	Jobe
Canada	Upper Firth River	762	1965	Drew & Shanks
Canada	Stoyoma Mountain	1950	2000	Pellatt, Smith, Mathewes, Walker, & Palmer
Canada	Canadian Rockies	NA	2000	Luckmann & Kavanagh
Chile	Puyehue National Park	1150-1350*	1977	Veblen, Ashton, Sschlegel, & Veblen
Chile	Puyehue National Park	NA	1979	Veblen
Chile	Balseiro Mountain	690	2002	Cuevas
China	Mount Khawa Karpo & Baima Snow Mountain	4300	2007	Baker & Moseley
China	Balang Mountain	3650-3750	2006	Shi, Körner, & Hoch

Table 1-1, continued.

Country	Location	~Treeline Altitude (m)	Year	Author(s)
France	North French Alps	2200-2300	1996	Carcaillet & Thinon
Germany	Black Forest	1200	2006	Lang
India	Central Himalayans	3300	1994	Garkoti & Singh
Japan	Japanese Alps	2450	2004	Gansert
Mexico	Pico de Orizaba	3990	1975	Lauer & Klaus
New Zealand	Multiple Sites Across New Zealand	600-1480	1992	Wardle & Coleman
Norway	Central Scandes	1000	1997	Hofgaard
Pakistan	Himalayas	NA*	1995	Schickhoff
Russia	Polar Ural Mountains	350	2005	Mazepa
South Africa	Döhne & Campagna Farms	830	1995	O'Conner
Spain	Tenerife of the Canary Islands	2100	1978	Höllermann
Spain	Spanish Pyrenees	2300	2004	Camarero & Gutiérrez
Sweden	Swedish Scandes	830	1987	Kullman
United States	Rocky Mountains in Colorado	3350	1872	Greene
United States	Northern Rocky Mountains Colorado	2590-3292*	1938	Griggs
United States	Sierra Nevada Mountains	3048-3353	1965	Clausen
United States	Brooks Range	760	1986	Cooper
United States	San Juan Mountains	3600	1991	Carrara, Trimble, & Rubin
United States	Medicine Bow Mountains	3300	2002	Hiemstra, Liston, & Reiners

altitudinal limit of closed canopy subalpine forests and the upper boundary is the uppermost altitudinal limit of arboreal vegetation (including krummholz). The horizontal linear distance spanning across the boundary may be only several meters or several hundred meters, depending upon the type of boundary being studied (i.e., Holtmeier's different classifications). The term subalpine parkland is invoked in some sections because many plant ecologists and biogeographers from the Pacific Northwest use and prefer that term.

1.1.4 Disturbance in the subalpine forest

Upper portions of the subalpine forest that comprise the lower part of treeline experience a multitude of disturbance events at various frequencies (Cullen et al. 2001). Of particular interest, are severe disturbances of a large magnitude and low frequency that denude the landscape of arboreal vegetation and effectively depress treeline to lower elevations, often necessitating the passing of decades or centuries for treeline to recover to its original altitudinal position (Peet 1981; Shankman & Daly 1988). These disturbances can drastically change the physiognomic appearance of a landscape and confound descriptions and definitions of treeline (Stueve et al. 2009). Indeed, they may also rival or exceed the importance of climate in dictating the altitudinal position of treelines (Peet 1981).

Stand-destroying fires are the most common large magnitude and low frequency disturbance capable of changing the altitudinal position of treeline at a large spatial extent, and depressing treeline altitudes several hundreds of meters or more (Peet 1981; Hemstrom & Franklin 1982). The upper reaches of the subalpine forest provide adequate fuel to generate a strong fire sometimes capable of spreading throughout treeline (Hemstrom & Frankling 1982). A significant large-scale event like this often removes viable seed sources from the highest elevations and makes post-fire reestablishment of trees a painfully slow and arduous process. This is because in order to have successful tree establishment in the denuded areas at higher elevations, viable seed must be simultaneously propelled distally beyond mature trees and upslope from mature trees surviving at lower elevations (Shankman 1984).

Some of these fires are caused naturally by lightning strikes, but anthropogenic fires (e.g., slash fire) are quite common as well (Peet 1981; Stueve et al. 2009). Stand-destroying treeline fires have been documented across the globe in places like the Rocky Mountains (Peet 1981) and Cascade Range (Stueve et al. 2009) of North America, the Spanish Central Pyrenees (Camarero et al. 2000) and Swiss Alps of Europe (Tinner et al. 1996), and the Andes of South America (Young & León 2007). Lack of fuel buildup at high elevations often limits the recurrence interval of these fires to 100 years or more, but once fuels reach a sufficient level the intensity of the fire can be quite severe and drastically modify the landscape for decades or centuries (Shankman 1984).

The relatively high prevalence of fires in the upper subalpine forest and treeline area has resulted in some scholars arguing that many treelines may never reach their true climatic limit (Peet 1981; Agee & Smith 1984). This rationale is based on the premise of slow treeline recovery times (e.g., challenges of dispersing seed upslope and shortened growing seasons at high elevations) and the likelihood that another fire disturbance will occur before treeline recovers to its original altitudinal position. Thus, many treelines may be in a perpetual state of recovery, constantly vying to reach their climatic limit before being subjected to another disturbance event, or experiencing an episode of climatic cooling that stymies reproduction. Many cases of treeline inertia or stability, which appear to be limited climatically, may actually result from orographic effects that prevent successful establishment at higher elevations. Climate remains important in the sense that favorable climatic conditions allow post-disturbance tree recovery to continue at a rapid rate.

Additional disturbances may influence treeline positions at more localized spatial extents, interacting with fire to produce peculiar patterns of arboreal vegetation in treeline landscapes. Insect infestations, avalanches, herbivory, landslides, rockslides, and lahars can suppress establishment and/or denude localized treeline areas of existing trees (Hemstrom & Franklin 1982; Brown 1994b; Walsh et al. 1994; Cairns & Moen 2004). However, in most cases, these events contribute to local treeline variability and fire tends to exert the most widespread influence on treeline positions (Hemstrom & Franklin 1982).

1.2 Study site

The Pacific Northwest encompasses all of Washington, Oregon, Idaho, and a large part of British Columbia. It also includes nearby areas in Montana, Alaska, California, and the Yukon Territory (Figure 1-3). The Coast Mountains, Cascade Range, Olympic Mountains, Columbia Mountains, and Rocky Mountains are all prominent physiographic features in the region. Some of the highest peaks surpass 4,000 m a.s.l. in elevation. Substantial altitudinal zonation associated with the mountains, and orographic influences on incoming moisture from the Pacific Ocean have generated distinct ecosystems. Dense old growth forest persists at low elevations (below ~1500 m a.s.l.) before grading to a patchy mosaic of tree clumps and alpine tundra at high elevations (above ~ 2200 m a.s.l.). The subalpine parkland (i.e., treeline) zone (~1500-2200 m a.s.l.) is unusually broad as well, often spanning across an elevation gradient of several hundred meters or more (Franklin & Dyrness 1988). The region also experiences abnormally heavy snowfall and holds the world record for the most snowfall in a year (2895.6 cm at Mount Baker) (Redmond 2000). Heavy yearly snowfall often is thought to play a critical role in suppressing the treeline on the windward sides of mountains in the area (Henderson 1974). A number of studies of the treeline in this region have been conducted over the last several decades (e.g., Henderson 1974; Agee & Smith 1984; Franklin & Dyrness 1988; Rochefort & Pedersen 1996; Stueve et al. 2009). Mount Rainier National Park is the focus of this dissertation.

Mount Rainier (4392 m) is a well-known and active volcano that dominates the landscape in Mount Rainier National Park. The park is positioned approximately 100 km southeast of Seattle, WA on the western slope of the Cascade Range (Figure 1-4). It comprises 95,356 ha of land ranging between old-growth forests at low elevations (~500-1500 m a.s.l.), treeline communities at high elevations (~1500-2200 m a.s.l.),

Figure 1-3: Regional perspective of the study area (Source: ESRI provided access to the map base layers).

alpine tundra immediately above, and the barren alpine landscape at the uppermost elevations (Rochefort & Peterson 1996). The alpine zone contains the largest area of glaciers in the continental United States, which nourish nine major rivers throughout the park with seasonal runoff. The aerial extent of the study area is defined by the northeast Mount Wow DOQQ on the western slope of Mount Rainier (Figure 1-4), which encompasses several hundred hectares of treeline. At this site, a 1930 fire severely burned extensive areas of high-elevation subalpine forest ranging approximately from 1500 to 1800 m a.s.l. in the vicinity of the North Puyallup River; effectively depressing treeline (Hemstrom & Franklin 1982). The burn arched up over a large ridge emanating from Mount Rainier and remnants of burned boles are still evident (Figures 1-5 & 1-6). Exploratory observations of 1970 satellite images and 2003 aerial photography indicated a substantial upward shift of treeline after the fire that would be suitable for addressing research questions with a combined landscape ecology, remote sensing, and GIS approach. Remnants of burned boles observed in the field and quantified on the 2003 aerial photography helped identify approximate historical treeline boundaries (Figure 1-5). Field observations in the fall of 2006 indicated there were no other potentially confounding disturbances that occurred in the study area.

The burned area includes numerous spurs that dissect broad south- and west-facing slopes containing complex microtopography, which can influence establishment patterns (Brown 1994a; Brown 1994b; Rochefort & Peterson 1996). *Abies lasiocarpa* is the most prevalent arboreal species. This species is a common invader after fires in treeline ecotones, with a preference for mildly xeric sites that are topographically sheltered (Shearer 1984; Miller & Halpern 1998). Wind- driven seed dispersal may carry seeds up to 80 meters beyond sexually mature trees (≥20 years old) (Noble & Ronco 1978). *Pinus albicaulis*, *Tsuga mertensiana,* and *Chamaecyparis nootkatensis* are also present, but much less abundant.

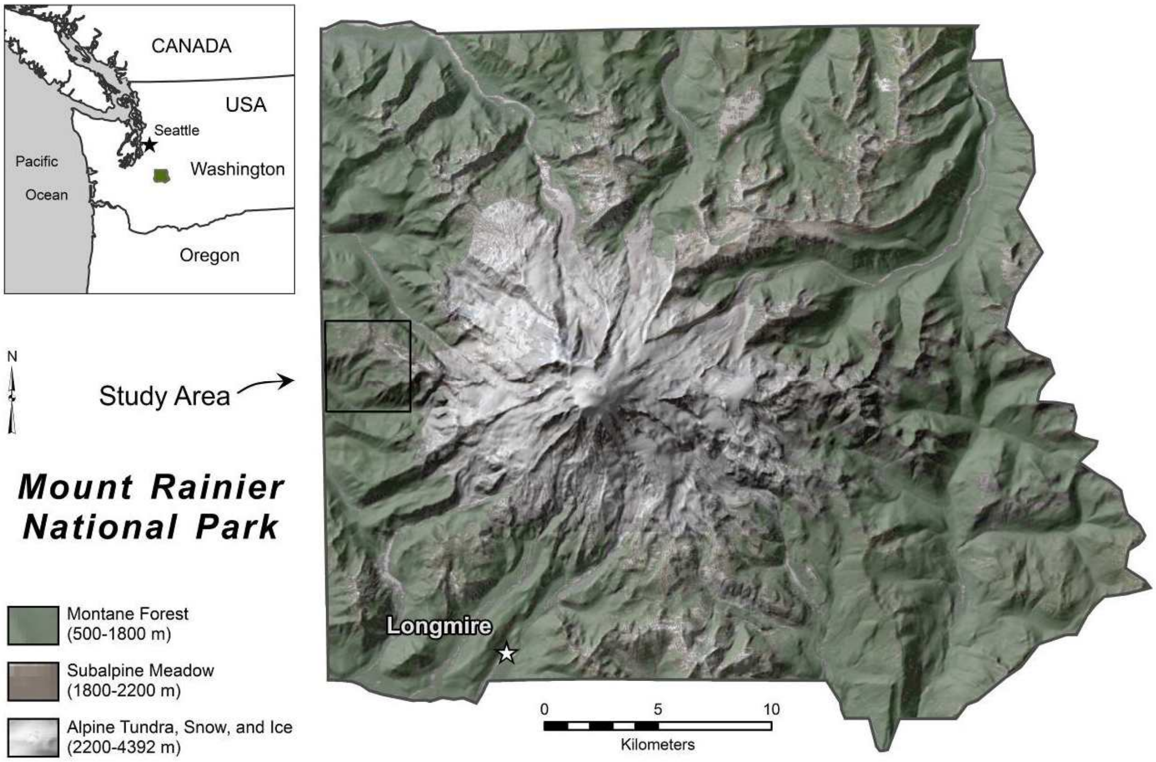


Figure 1-4: The park and study area as depicted by a modified September 2000 Landsat ETM+ satellite image from the University of Maryland Global Landcover Facility and a shaded 10 m USGS DEM. Digital image processing and manipulation of the data clearly highlights a series of distinct ecological zones. These zones span from the old montane forests at low elevations, subalpine meadows at middle elevations, and alpine tundra, snow, and ice at high elevations. This offers a classic example of altitudinal zonation of vegetation in mountainous locations.

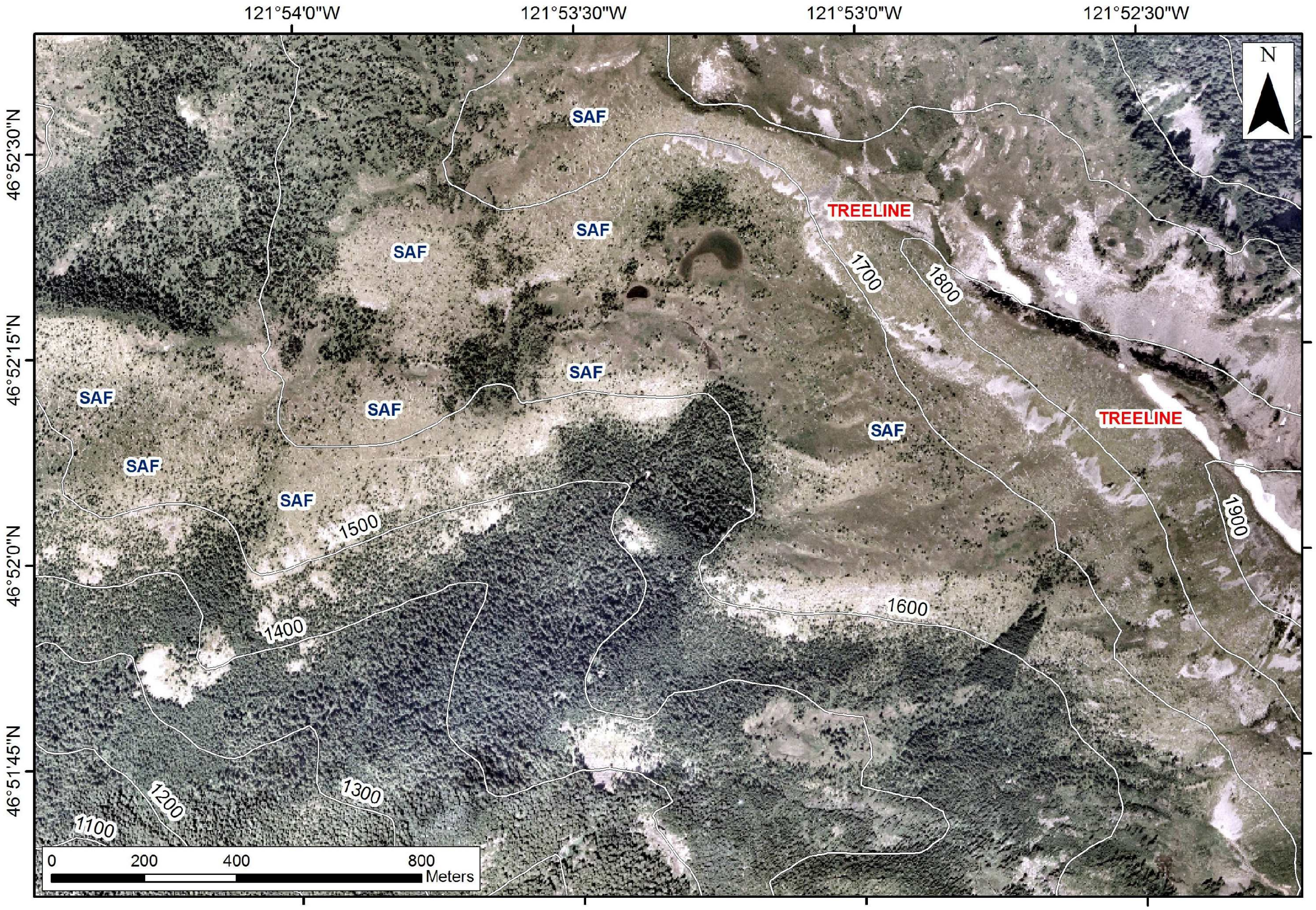


Figure 1-5: Map denoting the approximate location of treeline before the 1930 slash fire. Interpretations are based on observations of downed boles from the 2003 aerial photograph and in the field. Subalpine forest (SAF) similar to that near the 1400 m contour interval label probably dominated much of the study site (west-southwest part of the map) prior to the 1930 fire. Treeline was probably closer to 1700-1900 m in the northeastern portion of the map (Source: USGS).

1.2.1 Geology and topography

Mount Rainier is a nearly symmetrical stratovolcano with two craters at its summit. Deep valleys and many steep ridges consisting of Pleistocene and Holocene andesite scoured by glaciers dominate the landscape near the volcano (Figure 1-7). Topographic relief between the valleys and adjacent ridges often approaches 1000 m in these areas. Along with remnants of glacial drift (Crandell 1969); this has created

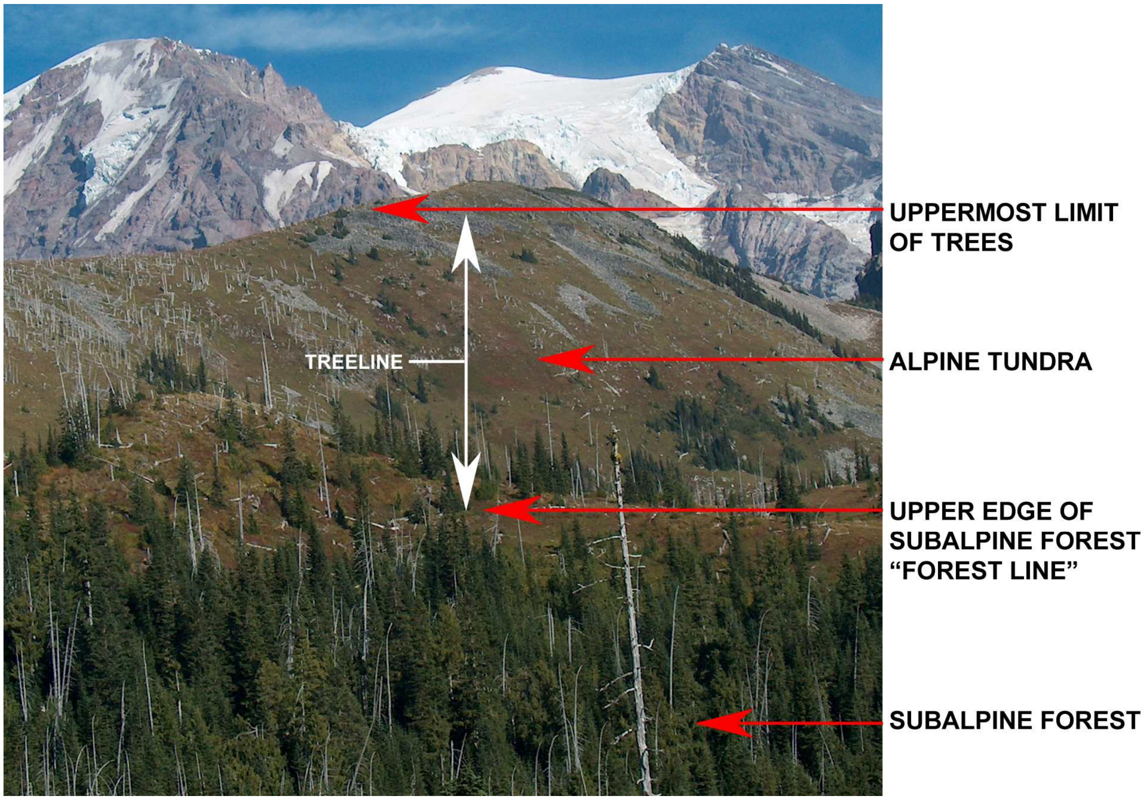


Figure 1-6: A portion of the ridge burned in 1930 that was photographed during fieldwork in September of 2006. The treeline and additional descriptive terms are identified in the image. Also, note the burned boles persisting on the ridge and throughout the subalpine forest in the foreground. These are the remnants of trees from the 1930 fire.

complex topographic features with widely variable microclimates that often influence patterns of treelines (Rochefort & Peterson 1996). Tertiary formations (e.g., Miocene and Oligoscene) are more frequent farther out from the volcano (Figure 1-7). They include several major geologic formations such as the Fifes Peak (andesite), Ohanapecosh (sandstone and breccias), and Steven's Ridge Formations (ash-flow tuffs)

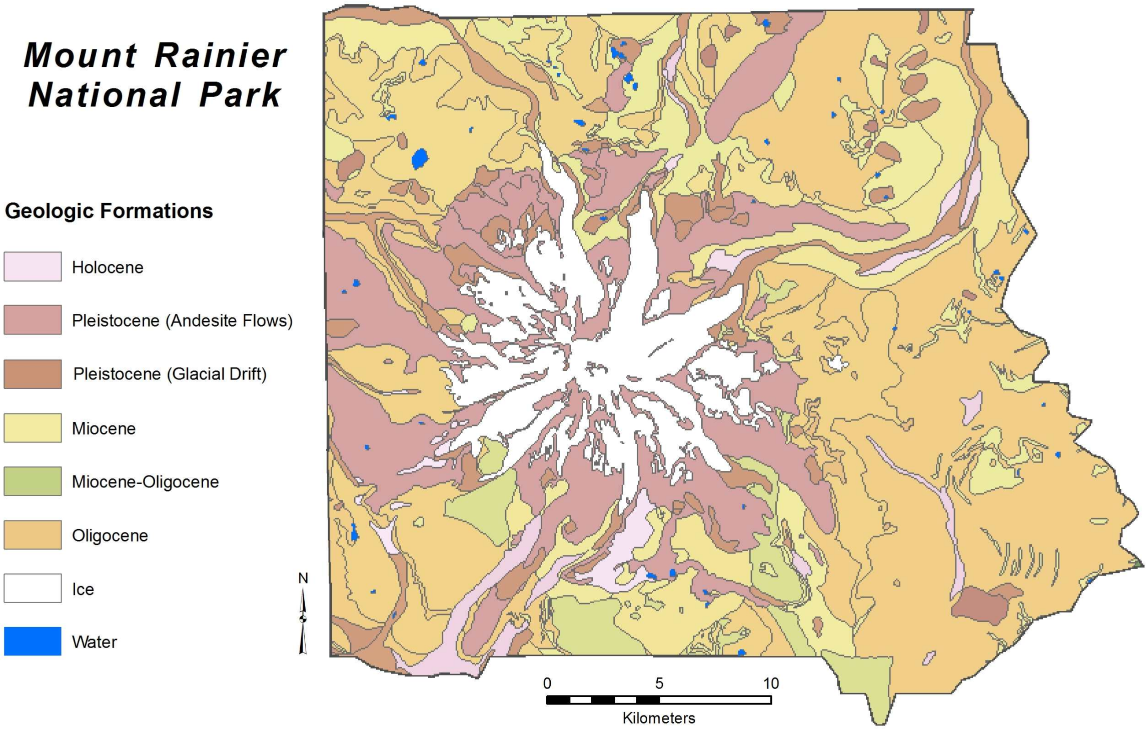


Figure 1-7: Major geologic formations in Mount Rainier National Park (Source: Washington State Department of Resources geology data). Fine-scale formations that would be difficult or impossible to detect on the map were intentionally excluded from the display. Most of the formations originate from sporadic periods of intense volcanic activity.

(Crandell 1969). A further prominent geologic stratum is the coarse-grained Granodiorite (approximately 12 million years old), which outcrops in the northwest, southeast, and northeast portions of the park (Fiske et al. 1963).

1.2.2 Climate

Climate in the region can best be characterized as humid temperate, with the majority of seasonal precipitation falling as snow or rain during cool winters (Bailey 1995) (Figure 1-8). Summers are often comparatively dry with warm temperatures (Hemstrom & Franklin 1982). Prevailing southwesterly winds create a pronounced orographic effect, resulting in heavy annual snowfall of 1000-2000 cm per year on the western slope of Mount Rainier (Hemstrom & Franklin 1982; Bailey 1995). The precipitation differential caused by the orographic effect is significant and influences the distribution of plant communities, but it is not as severe as the climatic changes between the west and east slope of the Cascade Range (Hemstrom & Franklin 1982).

Data from the Longmire weather station (elevation 842 m; Figure 1-4) (1978-2006) indicate average monthly temperature ranged from -0.3 °C in December to 16.0 °C in August, average annual precipitation (rain and melted snow) was 201.4 cm, and average annual snowfall was 344.2 cm. Snowpack may persist well into August on the western slopes, shortening the growing season to less than 100 days (Greene & Klopsch 1985) and contributing to relatively depressed treeline elevations (~1500 m a.s.l.)

compared to the eastern slopes (~2200 m a.s.l.) and other western USA treelines (~ 2200 m a.s.l. or higher) (Taylor 1922; Butler et al. 1994; Rochefort et al. 1994).

1.2.3 Soils

The parent materials of most soils in the park is the solid particulate matter ejected during volcanic eruptions from Mount Rainier or other surrounding volcanoes (e.g., tephra) and loose accumulations of materials at the base of hills from avalanche debris, talus piles, gravitational forces, and frost action (e.g., talus) (Hobson 1976). Little published data and no maps are available concerning specific soil types at fine scales. According to Thornburgh (1967), the most common soils in the southwestern vicinity of the park (near the study area) are brownish-colored podzols that are deep, well-drained, and coarsely textured. Some of these soils gradually grade into lithosols on the steeper slopes (Hemstrom 1979).

1.2.4 Flora

To date, over 890 species of vascular plants and 260 species of non-vascular plants have been documented in the park (National Park Service 2008). At least 149 exotic plant species also occupy riparian and travel corridors mostly below 1500 m a.s.l.. However, the focus here will be on the arboreal and herbaceous vegetation, particularly in the treeline ecotone.

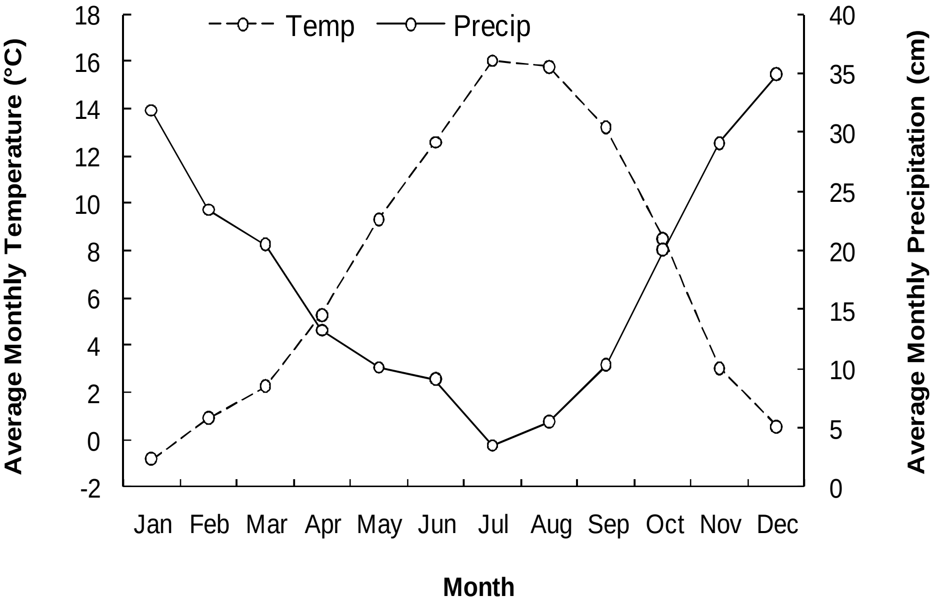


Figure 1-8: Climograph based on climate data (1978-2006) from the Longmire weather station (842 m a.s.l.) in the southwestern portion of the park.

The park contains precious remnants of old-growth coniferous forests (200-1000 years old) at low elevations (~500-1500 m a.s.l.) that used to occupy much of the Pacific Northwest (Kondratieff & Lechleitner 2002). These forests are mostly comprised of *Tsuga heterophylfa* and *Abies arnabilis* with the former being the dominant climax species up to about 900 m a.s.l. before slowly ceding to the latter (Hemstrom & Franklin 1982). Conifers that include *Abies lasiocarpa* (Figure 1-9), *Chamaecyparis nootkatensis* (Figure 1-10), and *Tsuga mertensiana* dominate the treeline (~1500 m a.s.l.) on the mesic western slopes of Mount Rainier. *Abies lasiocarpa* persists in extreme environments in the upper portions of the treeline either as upright or krummholz forms (Figure 1-11). *Picea engelmannii* and *Pinus albicaulis* (Figure 1-12) are most prevalent in the treeline (~2200 m a.s.l.) on the xeric eastern slopes (Rochefort & Peterson 1996).

Additional commonly found trees include *Abies procera, Pseudotsuga menziesii*, *P. monticola,* and *Thuja plicata.* Almost continuous pulses of increased tree establishment in the treeline have been documented in the western half of the park during periods of warm, dry summers (Franklin et al. 1971). Conversely, cool and wet summers have stimulated more discrete periods of tree establishment in these areas throughout the eastern half of the park (Rochefort & Peterson 1996).

Meadows in the treeline and alpine tundra are dominated by five major vegetation types including heath-shrub (e.g., *Cassiope mertensiana* and *Phyllodoce empetriformis*), lush herbaceous vegetation (e.g., *Valeriana sitchensis* and *Veratrum viride*), low herbaceous vegetation (e.g., *Antennaria lanata* and *Potentilla flabellifolia*), wet sedgeland (e.g., *Aster alpigenus* and *Carex nigricans*), and dry grassland (e.g., *Festuca viridula* and *Lupinus latifolius*) (Henderson 1974; Rochefort & Peterson 1996). Dry grassland vegetation is more common in the rain shadow on the eastern slopes of Mount Rainier and on exposed south-facing slopes than on the western slopes of Mount Rainier and sheltered north-facing slopes.

1.2.5 Subalpine parkland

The subalpine parkland is a distinctive feature of the Pacific Northwest and rarely found in other parts of the globe (Rochefort & Peterson 1996) (e.g., it does not fit well into any of Holtmeier's four treeline classifications). It is a remarkably wide treeline separating the subalpine forest and alpine tundra (Franknlin & Dyrness 1988).

Figure 1-9: *Abies lasiocarpa* (subalpine fir) photographed at the study site during fieldwork in September of 2006. Subalpine fir is the most abundant tree species at the study site.

Figure 1-10: *Chamaecyparis nootkatensis* (Alaska yellow cedar) photographed at the study site during fieldwork in September of 2006 (foreground). Abundance of Alaska yellow cedar is quite low at the study site.

Figure 1-11: A patch of *Abies lasiocarpa* (subalpine fir) in its krummholz form photographed during fieldwork in September of 2006.

Figure 1-12: A small cluster of *Pinus albicaulis* (whitebark pine) photographed at the study site during fieldwork in September of 2006. Whitebark pine is more pervasive on the eastern slope of Mount Rainier and not common at the study site.

The subalpine parkland is characterized by a mosaic of tree clusters interspersed with patches of dense herbaceous vegetation and often extends over an elevational gradient of300-400 m. Closed canopy forests comprise the lower boundary of this zone. Scattered upright arboreal vegetation or krummholz commonly demarcate the upper boundary. The patchy structure of the subalpine parkland is thought to be primarily maintained by the depth and duration of snowpack (Henderson 1974; Franklin & Dyrness 1988). The meadows of the subalpine parkland exhibit a particularly colorful display when they are in bloom and remain as a key attraction for park visitors. Treeline is used in lieu of subalpine parkland throughout this dissertation (except of special sections in Chapter II devoted to the subalpine parkland), but most plant ecologists and biogeographers from the Pacific Northwest prefer the use of subalpine parkland.

1.2.6 Disturbance

Fire is the predominant agent of disturbance in the park, having affected over 90% of the existing tree stands, including those at treeline (Hemstrom & Franklin 1982). Consequentially, this has created a patchy mosaic of forest with dissimilar stand ages, different successional stages, and a relatively rich species composition. The oldest stands in the park tend to occur at topographically sheltered locations below the treeline, on alluvial terraces, or in valley bottoms. Some of the youngest and most frequently replaced stands occur within or adjacent to the treeline (Hemstrom & Franklin 1982). Similar to other U.S. national parks, decades of fire suppression in the twentieth century have impeded the ~100-year recurrence interval for major fires and contributed to lush understory growth (Hemstrom & Franklin 1982). However, this practice has not been as detrimental to forest structure and species composition, as might be anticipated, because copious amounts of rain and snow contributed to dense understory growth well before the implementation of fire suppression strategies (Hemstrom & Franklin 1982). Nevertheless, fire is thought to play an important supplemental role in helping to maintain the herbaceous vegetation in the meadows of the treeline (in the case of severe fires) and also to facilitate tree establishment in these areas (in the case of light to moderate fires) (Rochefort & Peterson 1996). Continued fire suppression (especially the stand-damaging fires) and favorable climatic conditions may contribute to increased tree establishment rates in the treeline and accelerate the loss of subalpine meadows (Rochefort & Peterson 1996).

Other important disturbances include snow avalanches and lahars. Snow avalanches frequently occur in the park (every year), but they only influence about 7% of existing tree stands (Hemstrom & Franklin 1982). Lahars have influenced about 3% of existing tree stands and have provided some great examples of primary succession, but occur even less frequently than major fires (Hemstrom & Franklin 1982). Blow downs from windstorms and disease outbreaks from insects are also important considerations, but no large stands have been discovered and attributed to either of these disturbances (Hemstrom & Franklin 1982).

1.3 Research objectives

The research presented in this dissertation involves the use of remote sensing, geographic information science, spatial analysis, and multivariate statistical techniques in a landscape ecology framework to address treeline ecology and landscape ecology research questions at a site disturbed by fire in Mount Rainier National Park. Specific objectives are listed in the following three categories:

(1) Map vegetation and local site conditions.

(A) Utilize data from airborne and satellite remote sensing platforms to map areas of tree establishment.

(B) Use a LIDAR-derived DEM and maps of tree establishment to model environmental proxy data for temperature, soil moisture, erosion, snow cover, wind exposure, soil type, exposure, and positive ecological inertia.

(2) Assess and explain spatial patterns of tree establishment.

(A) Use landscape metrics to assess spatial patterns of tree establishment at various spatial extents throughout the treeline.

(B) Use multivariate statistics to determine what abiotic and biotic variables have exerted the most control on spatial patterns of tree establishment.

(3) Compare traditional logistic regression with hierarchical partitioning.

(A) Use both standard logistic regression and logistic regression within the hierarchical partitioning framework to determine if there are changes in the importance of local site conditions controlling tree establishment.

(4) Test for the presence of hierarchical patch dynamics.

(A) Exploit the high spatial resolution of the spatial data and resample to different spatial resolutions before subjecting data to multivariate statistics at each respective resolution to determine if importance of local site conditions changes.

1.4 Dissertation structure

Chapter II expands beyond the literature discussed in Chapter I and provides an overview of additional complementary literature. Section 2.1 reviews the ecology of the subalpine parkland and the importance of fire as a disturbance agent in the Pacific Northwest. Section 2.2 discusses the application of remote sensing in studying vegetation and important considerations for mountainous regions. Section 2.3 provides an overview of vegetation dynamics and landscape ecology.

Chapter III provides a substantive discussion of the methods used in this research. This includes the methods directly used in the manuscript-based chapters and supplemental details that could not be included in the methods of the manuscript-based chapters because of journal limitations on manuscript length.

Chapters IV-VI comprises the nucleus of this dissertation and they are structured as three separate manuscripts. Each chapter follows the standard topical manuscript sequence of introduction, methods, results, discussions, and conclusions. Chapter IV compares explanations of tree establishment patterns based on both standard logistic regression and logistic regression conducted within the hierarchical partitioning framework. Chapter V explains the spatial patterns of tree establishment at the treeline and places the resulting insight within the latest literature regarding change at subalpine forest-alpine tundra ecotones. Chapter VI assesses the potential influence various abiotic and biotic hierarchies may have on multivariate statistical analyses by modifying the spatial resolution of the variables utilized in explaining the spatial patterns of tree establishment.

Chapter VII reemphasizes the conclusions from chapters IV-VI in the initial section. This chapter goes on to address necessary assumptions and potential influences of external factors in addition to offering some suggestions for improvements.

CHAPTER II

ECOLOGY, REMOTE SENSING, AND VEGETATION DYNAMICS

Chapter II enhances and expands beyond the literature presented in Chapter I. Section 2.1 explains the ecology of the subalpine parkland and the importance of fire as a disturbance agent in the Pacific Northwest. Particular attention is given to various explanations of the spatial mosaic of arboreal and herbaceous vegetation of the subalpine parkland. Section 2.2 provides a brief overview of remote sensing and vegetation before addressing the utility of remote sensing in studying arboreal vegetation of mountains. Section 2.3 expands upon the introduction and discusses landscape ecology as an approach for studying vegetation dynamics.

2.1 Subalpine parkland ecology

The unique subalpine parkland landscape of the Pacific Northwest (Figure 2-1) has piqued the curiosity of tourists for over 100 years, particularly the wildflowers that occupy the open meadows (Rochefort & Peterson 1996). Consequently, park managers and ecologists have also devoted significant amounts of time, money, and energy to studying the subalpine parkland in an attempt to understand its peculiar spatial mosaic of vegetation (Agee & Smith 1984; Miller & Halpern 1998). Mount Rainier National Park has been the focus of much of this research (Rochefort & Peterson 1996).

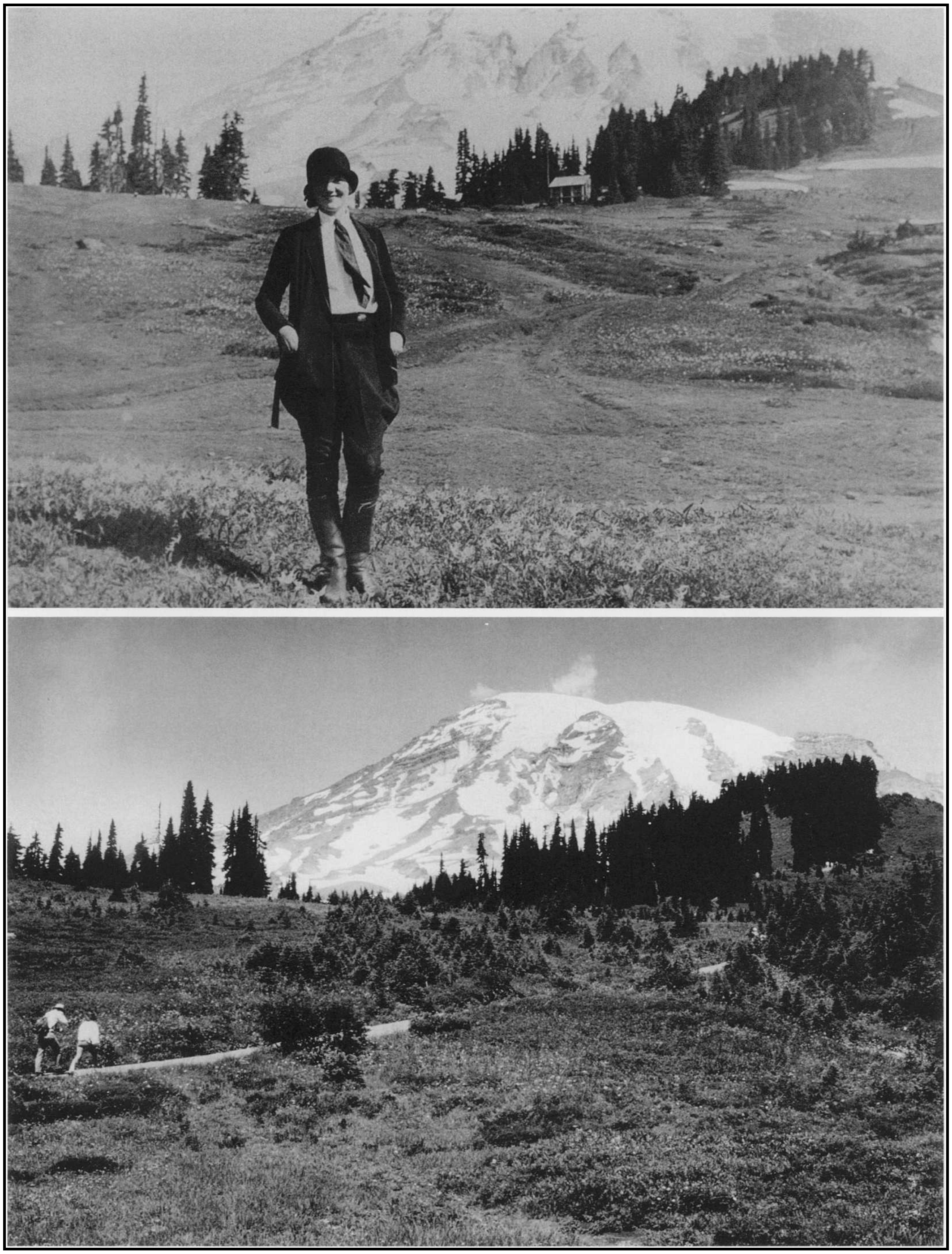


Figure 2-1: Photographs of subalpine parkland in the Paradise area of Mount Rainier National Park as observed in 1929 (top) and 1992 (bottom) (Source: courtesy of Rochefort & Peterson, 1996). Note how the subalpine parkland is characterized by a patchy mosaic of herbaceous and arboreal vegetation with increased tree establishment in the 1992 picture.

The subalpine parkland is an unusually wide and conspicuous treeline ecotone between the subalpine forest and alpine tundra that often spans an elevation gradient of several hundred meters or more (Franklin & Dyrness 1988). Closed canopy forests predominate throughout the lower border of this ecotone (~1500-1800 m a.s.l.), before slowly ceding to patchy forest and eventually sparsely distributed individuals or clumps of arboreal vegetation near the upper border (~1800-2200 m a.s.l.). Most of the attention from ecologists has remained focused on explaining the spatial patterns of tree patches or individual trees, in the hopes of predicting how the subalpine parkland may respond to climate changes (Rochefort & Peterson 1996). It is clear that this is a worthwhile endeavor, especially considering that the subalpine parkland is extremely dynamic and constantly changing over various temporal and spatial scales (Miller & Halpern 1998). Explaining how the subalpine parkland changes (i.e., how it experiences infilling and how it moves upslope) is of paramount importance to ecologists and park managers (Rochefort & Peterson 1996). The presentation of the ecology of the subalpine parkland is primarily from the aforementioned perspective.

2.1.1 Origin and broad controls on spatial patterns

Uneven glacial recession at the end of the Pleistocene and relatively infrequent fires (light to moderate in intensity) were the most likely contributors to the creation of the subalpine parkland (Hendersen 1974). Persistent remnants of receding glaciers most likely inhibited tree establishment and favored the eventual generation of meadows in what were typically moist and cool environments. Mesic soils exhibit a tendency to remain unusually cold throughout the growing season at high elevations and inhibit tree establishment (Holtmeier 2003). A lack of light to moderate fires (e.g., those that do not destroy substantial quantities of trees) probably facilitated meadow creation as well because undisturbed meadows tend to be more resistant to encroaching tree establishment. Whereas severe fires often disturb the meadow in addition to denuding the adjacent areas of sexually viable trees, effectively lowering the altitudinal position of the subalpine parkland in many instances (Hemstrom & Franklin 1982). Although extensive areas of burned meadows may be more favorable for establishment under these circumstances, reliable sources of viable seed are often lacking. In the absence of disturbances and in the presence of a climatic stasis, the broad patterns and altitudinal positions of the subalpine parkland spatial mosaic observed today are thought to be primarily maintained by imposed limitations on tree establishment and growth from (1) high summer temperatures (in xeric locations); and (2) season-shortening snowpack (mesic locations) (Sanscrainte et al. 2003).

2.1.2 Influences of climate, weather, and broad geographic position

At a regional scale, fluctuating weather and/or climatic conditions appear to play a role in facilitating tree establishment in the subalpine parkland; resulting in substantial meadow infilling and upslope advancement of trees (Rochefort & Peterson 1996). Mesic locations (e.g., western slope of Mount Rainier) display a propensity for establishment during abnormally warm and dry summers or in the midst of general climatic warming (Franklin et al 1971; Kearney 1982; Rochefort & Peterson 1996). These conditions typically prolong the growing season (e.g., snow melts more quickly) and the generally mesic environment usually provides ample moisture to sustain pulses of establishment (Rochefort & Peterson 1996). Field reports throughout the twentieth century provide evidence of pulses of increased tree establishment on the comparatively mesic western slope of Mount Rainier during warm, dry summers (Rochefort & Peterson 1996). Conversely, xeric locations (e.g., eastern slope of Mount Rainier) tend to experience increased establishment rates during cool/wet summers or slightly cooler/wetter climatic conditions (Rochefort & Peterson 1996). Moisture is often limiting in these areas along with extreme soil temperatures (Baig 1972). Thus, warm and/or dry conditions rarely facilitate establishment and cool/wet conditions are usually necessary to sustain any establishment pulses. Field reports of increased establishment rates on the eastern slope of Mount Rainier are common during cool/wet summers (Rochefort & Peterson 1996).

2.1.3 Influences of local site conditions

Vegetation type, topographic relief, microsite variability, proximity to existing tree clumps, and source of ecotone perturbation appear to influence patterns of tree establishment when favorable climatic or weather conditions persist and facilitate pulses of establishment (Agee & Smith 1984; Rochefort & Peterson 1996). For instance, heath-shrub communities in subalpine parkland meadows on the western slope of Mount

Rainier promote increased rates of establishment (when compared to other vegetative communities in the meadows) by prolonging the growing season and moderating temperature or moisture extremes with their elevated ground surfaces (Rochefort & Peterson 1996). A similar trend occurs on the eastern slope of Mount Rainier, although it is much less pronounced (Rochefort & Peterson 1996). Reduced establishment success rates often occur in other meadow communities, such as dry grasses.

In terms of topography, convex and shaded locations at comparatively low elevations are more likely to experience establishment (Agee & Smith 1984; Rochefort & Peterson 1996). Convex surfaces accumulate less snow, tend to exhibit longer growing seasons, and are immune to oversaturation from too much water. Shaded locations also offer protection from extreme temperature variation, which also appears to favor seedling survival. Additionally, less extreme climatic conditions lengthens the growing season at low elevations, which favors establishment. Less is known about slope angle, but it appears that moderate slope angles favor establishment because here meadow communities are less likely to competitively exclude trees (as is common at gentle slope angles) and soils are further developed (compared to steep slope angles).

A suit of microsite conditions also appears to influence establishment patterns (Little et al. 1994; Rochefort & Peterson 1996). Stumps or downed boles provide protection from temperature extremes and often exhibit clumps of newly established trees around them. Patches of particularly well-drained soils also promote establishment. Lengthier growing seasons typify well-drained soils and they are much less likely to remain cool and wet during key stages of seedling development. Ameliorated conditions offered by other debris, such as individual boulders, also seem to favor establishment.

Close proximity to existing trees has been widely reported to favor the establishment of more trees in the subalpine parkland (Agee & Smith 1984; Rochefort & Peterson 1996). It is thought that a combination of abundant quantities of nearby seed and positive feedback factors from existing trees may enhance establishment in these locations. Nearly ubiquitous coverage of seed dispersal greatly increases the odds of a tree becoming successfully established. Existing trees also offer protection from temperature extremes and ameliorate the local site conditions, thus bolstering the probability of seedling survival even more (Stueve et al. 2009). However, most of the evidence for positive feedback factors is largely circumstantial and the result of drawing conclusions based on observed associations in space. Additional research is necessary to directly test this assertion.

The type of ecotone perturbation has also been found to be an important factor in influencing tree establishment patterns in the subalpine parkland (Rochefort & Peterson 1996). Locations disturbed by severe fires tend to experience establishment adjacent to sexually mature trees that survived the fire; with trees only gradually invading open meadows (Agee & Smith 1984; Little et al. 1994). Conversely, increased establishment rates tend to be facilitated by light to moderate fires because this tends to create suitable germination sites in what was formerly lush herbaceous cover. Establishment triggered by climate change is also generally more widespread in the meadows and mostly controlled by topographic variability or vegetation type (Douglas 1972; Kearney 1982).

There certainly is a rich and descriptive literature regarding subalpine parkland ecology. However, most studies have previously been conducted at restricted spatial scales and only considered a few of the multiple abiotic and biotic variables that may influence spatial patterns of arboreal vegetation. A cumulative synthesis that considers multiple variables and disparate scales is lacking. Formulating and executing such an approach is a necessary precursor to incrementally advancing our understanding of how the subalpine parkland changes over space and time and, ultimately, synthesizing a better conceptual model.

2.2 Remote sensing and vegetation mapping

The vast majority of research approaches employed for studying tree establishment and other ecological processes have consisted of field-based techniques utilizing dendroecology and classic plant classification procedures in plots or belt transects (e.g., Agee & Smith 1984; Rochefort & Peterson 1996; Daniels & Veblen 2003). However, remote sensing approaches (i.e., using devices to record data or information about phenomena without being in contact with them) are nevertheless becoming more popular and are being touted as an invaluable complement to previous and ongoing field-based research (Gillespie et al. 2009; Kennedy et al. 2009).

Useful applications of remote sensing in biogeography and ecology were overtly recognized and explored in the scientific literature several decades ago. Some of these uses included assessing vegetation vigor (e.g., Tucker 1979), quantifying biomass (e.g., Tucker 1985), and terrestrial mapping of physiognomically distinct vegetative communities (e.g., Driscoll et al. 1978; Komárková & Webber 1978). Remote sensing platforms exploiting the visible and near-infrared portions of the electromagnetic spectrum were touted as being particularly useful for geographers in studying patterns and processes on the landscape (Cooke & Harris 1970). Prominent scholars continue to posit that remote sensing techniques may be especially useful for facilitating explanations of classic ecological and biogeographic questions regarding hierarchical patch dynamics and spatial dependencies (Millington et al. 2002). Although, other scholars also emphasize that remote sensing science is clearly not a panacea, and that its utility primarily hinges upon the types of research questions being asked (e.g., Jensen 2005). Spectral reflectance, spatial resolution, and classification techniques are particularly crucial considerations when attempting to answer specific ecological or biogeographic research questions in alpine environments; especially when mapping data of physiognomically distinct ecological communities from historical panchromatic imagery and contemporary aerial photography (Driscoll et al. 1978).

2.2.1 Spectral approaches

The electromagnetic spectrum encompasses different types of radiation at particular wavelengths (Figure 2-2). The majority of remote sensing studies conducted at treeline utilize the visible (e.g., Klasner & Fagre 2002; Resler et al. 2004) and/or infrared (e.g., Brown 1994b; Hoersch et al. 2002) portions of the electromagnetic spectrum and have been undertaken within the last 10-20 years. This distinctive trend corresponds with the exponential growth of remote sensing- and GIS-based studies over similar temporal periods. The types of data being utilized can mostly be attributed to the fact that the majority of suitable archived data (e.g., several decades old, or more, to document incremental ecological change in remote locations) comprise panchromatic, color, or infrared images. Archived hyperspectral data and other remotely sensed images remains of limited use for exploring change at treeline, but definitely appears promising for future studies.

Fortunately, treelines are physiognomically distinct boundaries with adequate spectral variability between arboreal vegetation, herbaceous meadows, and soil in the visible and infrared portions of the electromagnetic spectrum (Figure 2-3). Note how subalpine fir and meadow exhibit distinctive spectral spikes with sharp declines, whereas soil has a more steady and gradual curve. In healthy plants, the molecular structure of chlorophyll pigments in the palisade parenchyma cells absorbs most visible light (for photosynthetic purposes), but reflects a comparatively higher amount of electromagnetic energy between 500-600 nm. This phenomenon produces the green color in healthy leaves and a small spike in the spectral curve near 550 nm (Tucker 1979). Conversely, the molecular structure of the spongy mesophyll reflects most near-infrared electromagnetic energy. This is an evolutionary advantage that prevents sensitive proteins from being denatured and produces the pronounced spike in the spectral curve near 700 nm (Tucker 1979). Water tends to absorb radiation in the middle-infrared portion of the electromagnetic spectrum, but absorption is comparatively low near 1700 nm and contributes to a spike in reflectance (Jensen 2005). However, this spectral signature is usually blurred when vegetation is stressed and internal water levels are depressed. Finally, the physical structure and design of the foliage in vegetation can also alter spectral reflectance curves (Tucker 1985). This phenomenon explains the gap in spectral reflectance between alpine meadow and subalpine fir.

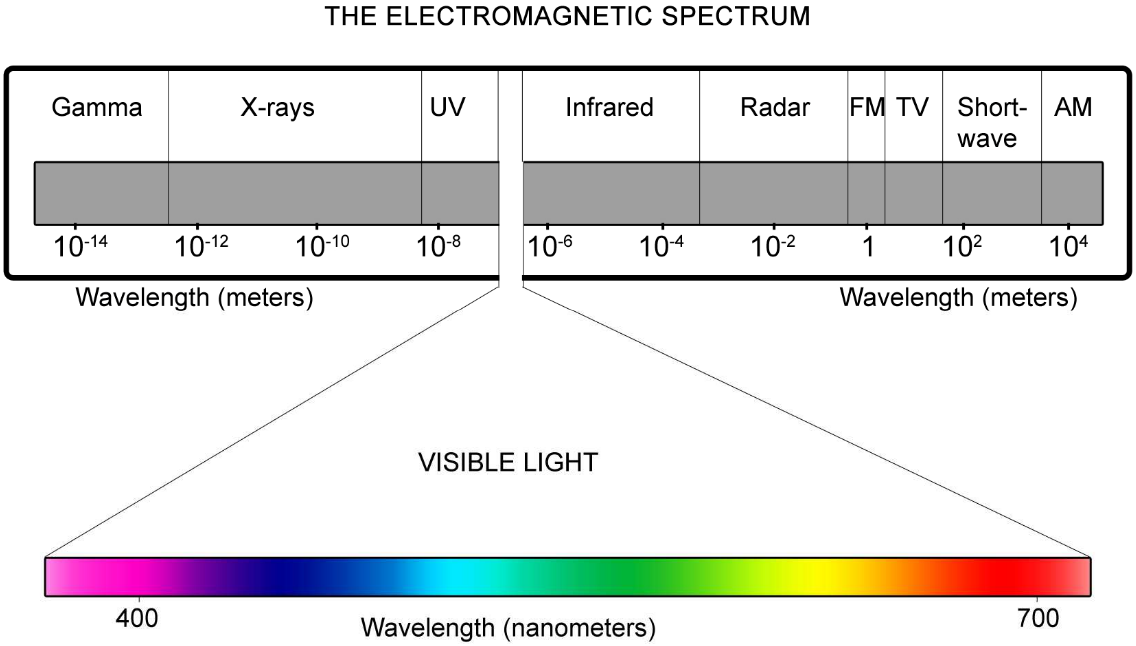


Figure 2-2: Wavelengths of the electromagnetic spectrum (Source: information used to create this graph was acquired from Jensen, 2005).

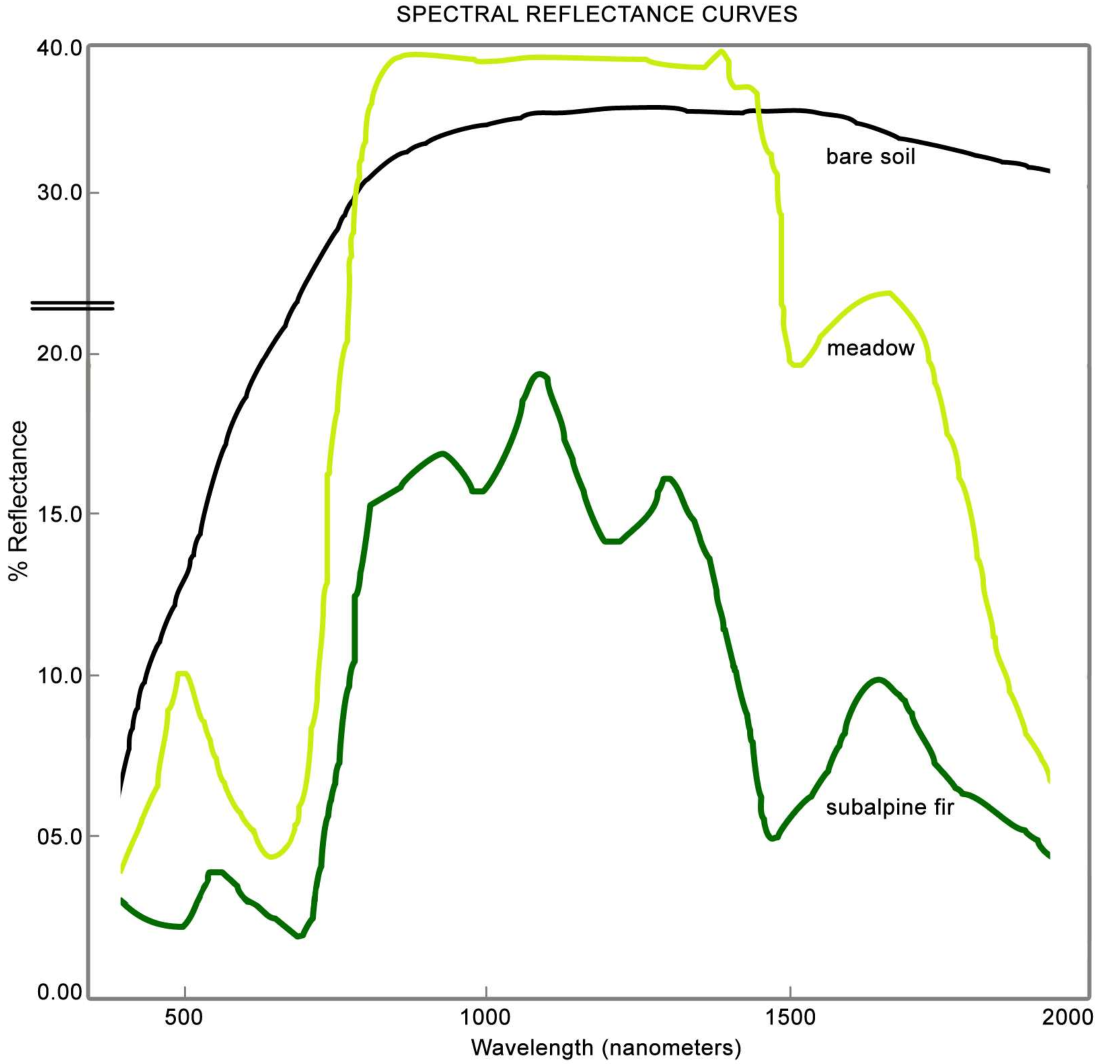


Figure 2-3: Spectral reflectance curves of *Abies lasiocarpa* (subalpine fir, the most common tree species at the study site), bare soil, and herbaceous meadow (Source: information used to create the graph was acquired from Raymond et al., 1998 and Zagajewski & Sobczak, 2003).

2.2.2 Considerations of spatial resolution

Most remote sensing studies performed at treeline have utilized aerial or satellite remotely sensed data with fine spatial resolutions between 0.5 m and 2.0 m (e.g., Klasner

& Fagre 2002; Resler et al. 2004; van Oosterom et al. 2006). Others (e.g., Brown 1994b; Butler et al. 2003) have taken advantage of the increased spectral resolution provided by satellite remote sensing systems that capture data with relatively coarse spatial resolutions (e.g., Landsat TM/ETM+ at 30 m).

Spatial resolution provides a measure of the smallest distance separating two objects on the landscape that can be resolved by the respective remote sensing systems (Cooke & Harris 1970). To detect specific objects of interest, the spatial resolution should generally be at least less than one-half the size of the object of interest (Jensen 2005). For example, aerial photography and declassified reconnaissance images with relatively high spatial resolutions (e.g., 0.5-2.0 m) are capable of discerning some of the more mature trees in treeline environments (Figure 2-4), although only clustered patches of saplings may be detectable. This is a useful approach for detailed studies of pattern and process where spatially explicit maps of the landscape are necessary. Alternatively, coarser spatial resolutions associated with Landsat TM/ETM+ data (e.g., 30 m for the multispectral bands) and other remote sensing platforms with broad coverage are only able to discern patches of mature trees. Inevitably, areas of adjacent meadows may be incorporated with some of these coarse resolutions (Figure 2-4), depending upon the statistics involved with the classification scheme. This approach is advantageous when mapping large areas, but it is usually performed at the expense of fine-scale accuracy.

Considering that spatial dependencies are exceptionally strong in treeline environments, the selection of an appropriate remote sensing system with a spatial resolution that is best suited for answering stated research questions is especially important (Walsh et al. 1994). Landsat TM/ETM+ or SPOT images may suffice in some instances, but it might be necessary to exploit the high spatial resolutions of aerial photography or satellite images (e.g., 0.5-2.0 m) in other cases.

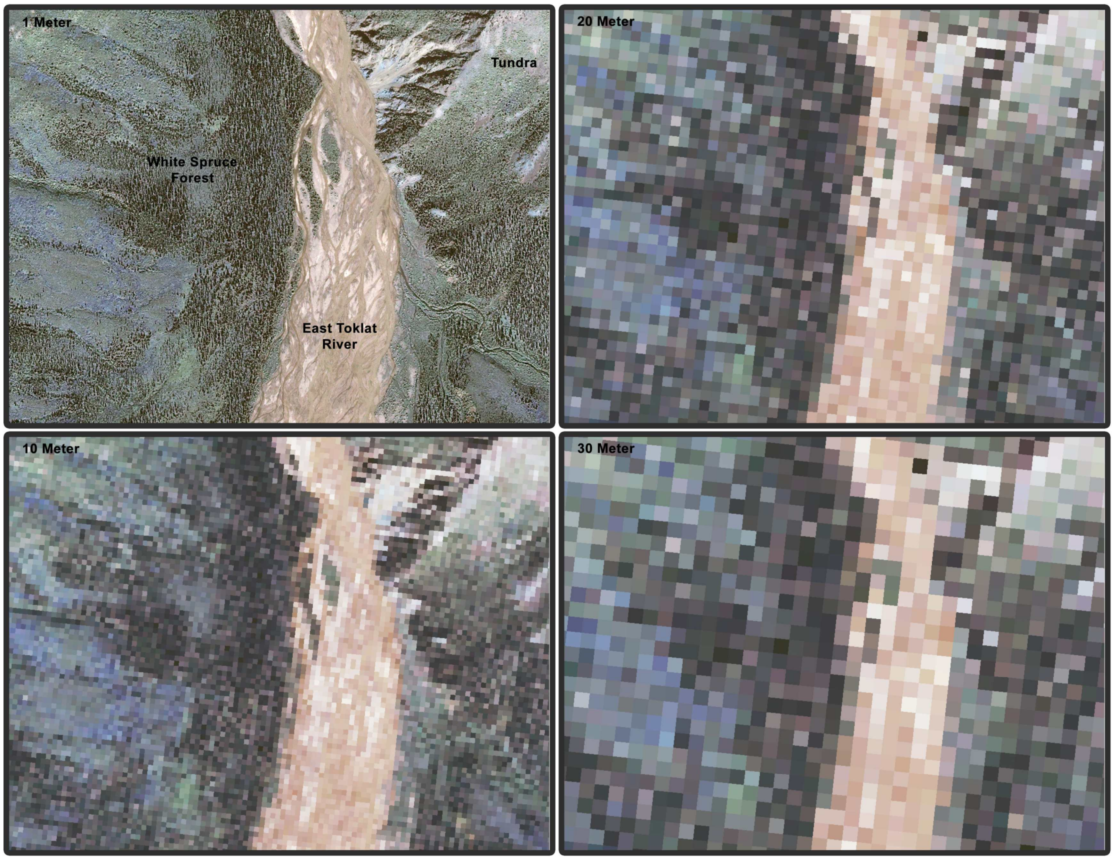


Figure 2-4: White spruce forest and tundra denoted by a series of different spatial resolutions near the East Toklat River in Denali National Park and Preserve, Alaska. Note how it is possible to distinguish between individual trees and stream braids in the 1-m image. Alternatively, the boundary between forest and tundra progressively blur in the spatially degraded images and stream braids are nearly completely obscured (Source: the National Park Service kindly provided a 1 m pan-sharpened 2005 IKONOS image that was resampled to increasingly coarser images to create this figure).

2.2.3 Classification approaches

Determining how to extract features with useful and reliable information from remotely sensed data is a crucial and sometimes daunting consideration when conducting research in treeline environments. Traditionally, hard and fuzzy classifications were the two preferred choices, but object-oriented classifications are becoming increasingly popular (Laliberte et al. 2004). Brown (1994b) successfully employed an unsupervised hard classification in Glacier National Park and others have espoused this approach (e.g., Walsh et al. 1994; Klasner & Fagre 2002) or opted for a supervised hard classification (e.g., Resler et al. 2004; Stueve et al. 2009). Conversely, Hill et al. (2006) tested a fuzzy classification at treeline in Hohe Tauem Mountains National Park in Austria and found that it performed well. Geddes et al. (2005) also demonstrated that object-oriented classifications can be useful in another study at Glacier National Park. Each approach is replete with its own strengths and it would be imprudent to proclaim one superior to the other (Jensen 2005).

Hard classifications are derived from the spectral characteristics of individual pixels, which are selectively assigned to the most appropriate class based on unsupervised or supervised classification criteria (Laliberte et al. 2004). These procedures typically result in a map with discrete classification categories (e.g., forest, bare rock, meadow, and water) (Figure 2-5). Hard classifications driven by Boolean logic are practical for quantifying discrete vegetation types, generating sharp boundaries between features, and conceptualizing treeline environments. However, critics assert that these classifications provide an inadequate representation of transitional areas that often pervade treelines (Hill et al. 2006).

Soft or fuzzy classifications rely on the partitioning of feature space via individual pixels that have graded values (e.g., between 0 and 1) for a specified number of classes based on supervised or unsupervised classification techniques of spectral reflectance values (Benz et al. 2003). This approach tends to soften the sharp edges of hard classifications and blur the boundaries between vegetation types (Figure 2-6). Advocates contend that fuzzy classifications are best able to represent treelines and that

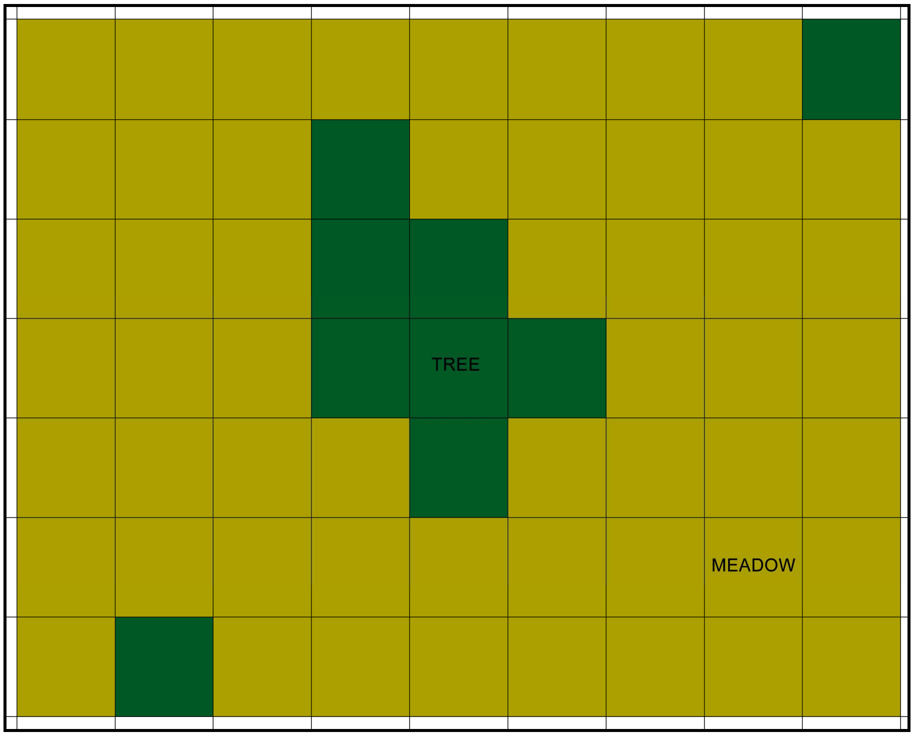


Figure 2-5: Conceptual example of a hard classification with a binary mapping scheme of trees (green) versus meadows (light brown).

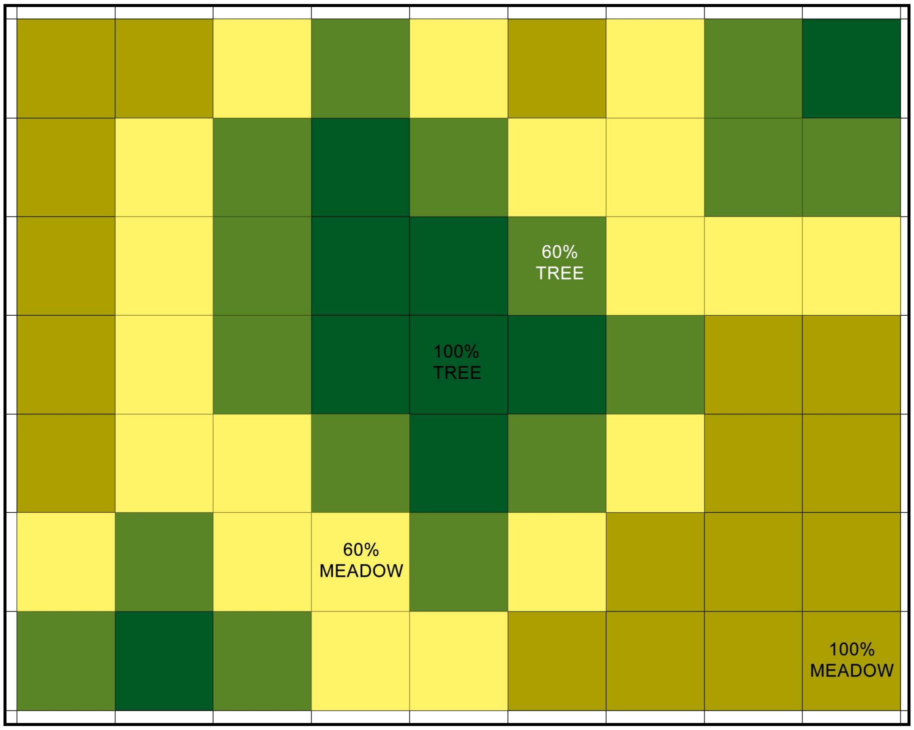


Figure 2-6: Conceptual example of a fuzzy classification with a graded mapping scheme for the same area as Figure 2-5. Trees (green) and meadows (light brown) continue to be identified, but note how the edges are 'softened' where there is a tree/meadow mixture.

one might be able to glean additional ecological insight from the more thorough representation of these transitional areas (Hill et al. 2006). However, a transitional 'fuzzy' area may also complicate attempts to make ecological interpretations at treeline due to decreased classification accuracy in the transitional areas.

Object-oriented classifications forgo the individual per-pixel classification and employ multiresolution image segmentation techniques that breaks the scene down into homogeneous patches or 'objects' (Laliberte et al. 2004). The statistical characteristics of the respective objects are then used to classify the objects via standard techniques (e.g., fuzzy classification). Object-oriented techniques are commonly applied to multispectral remotely sensed images with high spatial resolutions (e.g., IKONOS or QuickBird) (Geddes et al. 2005). These techniques offer an advantage when trying to discern landscape features that have similar spectral properties, but different patch shapes.

2.3 Vegetation dynamics and landscape ecology

Vegetation dynamics is concerned with the spatial distribution and temporal dynamism of flora in relation to each other and their surrounding environment. Some have speculated that the earliest humans must have had an understanding of vegetation dynamics and their physical surroundings on the landscape in order to adequately support their nomadic lifestyles (Lomolino 2001). Indeed, it seems survival would have been hindered without at least a basic understanding of these topics. However, formal documentation of such knowledge did not occur until much later.

Carl Ludwig Willdenow was a well-known German botanist from the eighteenth and nineteenth centuries and one of the first scientists to formally recognize and appreciate vegetation dynamics (Willdenow 1805). He was particularly aware of, and intrigued by, latitudinal and altitudinal variations in species diversity (Lomolino 2001). He suggested that temperature, the length of the growing season, soil development or lack thereof, moisture stress, and drought stress all might contribute to explaining some of these spatial variations. The German naturalist and geographic explorer Alexander von Humboldt (mentored by Ludwig) carried on and expanded upon some of Ludwig's work (e.g., von Humboldt 1807). He was also trained as a botanist, but noticed and became intrigued with topics such as altitudinal zonation of vegetation and latitudinal variability of species richness (von Humboldt 1807; Hawkins 2001). He didn't employ the use of contemporary terms such as 'diversity' and 'species richness', but he clearly appreciated them and recognized spatially explicit changes of flora corresponding with various environmental variables throughout the landscape (Hawkins 2001). His observations and insights were important contributors to the disciplinary development of ecology, biogeography, and ultimately landscape ecology; all of which continue investigations of vegetation dynamics at the present time (Turner 1989; Hierro et al. 2005).

The British naturalist, explorer, geographer, and biologist Alfred Russell Wallace was another nineteenth century academic who was intrigued by the peculiar spatial distribution of plants across the landscape (Wiens & Donoghue 2004). He demonstrated an appreciation for vegetation dynamics when trying to explain the geographic distributions of various fauna and the importance of their respective habitats (Wallace 1876). He was also well-acquainted with Charles Darwin and a stout advocate of natural selection. Today he is known by many to be the co-discoverer of natural selection and the father of biogeography (Peck 2003).

During the late nineteenth and early twentieth centuries, future ecological icons Frederick Clements (1897, 1916) and Henry Gleason (1926) were developing groundbreaking theories concerning vegetation dynamics while conducting scientifically rigorous field research. Clements' field research in Nebraska and the western United

States helped to mold and shape his theory of succession, which stated vegetative communities were primarily controlled my macroclimatic factors and would slowly change or mature to a climax state after a disturbance. Clements' emphasis on temporal vegetative change and largely organismic view of vegetation dominated ecological thought in the early to middle twentieth century (Turner 1989). Conversely, Gleason challenged Clements' theory and emphasized the importance of individualistic relationships between different species in concert with both abiotic and biotic spatial heterogeneity (Turner 1989). Gleason was largely ignored until the 1950's, when the work of Robert Whittaker and others (e.g., Watt 1947; Curtis 1959) finally helped to ease the grip of the firmly entrenched Clementsian paradigm with a Gleasonian one (Westman & Peet 1981). Some of Watt's work also started to raise questions concerning spatial scales and variability across the landscape; effectively setting the stage for future disciplinary advancement in studying vegetation dynamics.

By the late 1960's, Robert MacArthur and Edward Wilson had developed the theory of island biogeography (1967). In this context, an island could be any area of habitat on the landscape surrounded by an area of unsuitable land for a particular species. The theory proposes that immigration and extinction are the two most important factors influencing the number of species existing on an undisturbed island. Proximity to colonizers is most likely to affect the former and island size the latter. Although modern island biogeography was mainly developed from experiments with a few mobile animal groups, it stimulated research concerning vegetation dynamics (e.g., van der Maarel

1988) and helped to facilitate spatially heterogeneous conceptualizations of landscapes (Lomolino 2001).

In the early 1980’s, landscape ecology evolved as a new ecological paradigm that considered landscapes to be ecological units comprised of the spatially heterogeneous patch-corridor-matrix (Forman & Gordon 1981; Forman 1995). The term *landscape ecology* was used well before the 1980's by the German geographer Carl Troll (1939). However, it took over 40 years for Watt’s (1947) seminal linkages of space, time, and scale across the landscape (Turner 1989) and novel landscape conceptualizations from the theory of island biogeography (Lomolino 2001) to percolate throughout the scientific community and coalesce into a new paradigm. Landscape ecology appeared to show promise in providing a unique and useful approach in studying vegetation dynamics (Turner 1989).

In essence, landscape ecology is concerned with broad spatial scales and the effects of spatial patterns and processes in ecological systems (Turner 1989). Spatial heterogeneity (i.e., spatial variability in the patch-corridor-matrix) is the central underlying tenet of landscape ecology (Turner 1989; Forman 1995). Patches are distinct ecological communities surrounded by a matrix with dissimilar communities and corridors are path lines often interspersed throughout or on the perimeter of the matrix (Forman & Gordon 1981) (Figure 2-7). There are three important considerations when investigating the spatial heterogeneity of a landscape. These include structure (e.g., spatial distribution of species or functional group in relation to the components of the patch-corridor-matrix), function (e.g., flow of energy or organisms between the components of the patch-corridor-matrix), and change (e.g., structure and function varying over time) (Turner 1989).

Figure 2-7: An example of the patch-corridor-matrix along a braided stream supplied with water from glacial melt. The picture was taken facing west across the East Fork Toklat River about 8.5 km north (following the river bottom) of the eastern park road in Denali National Park and Preserve.

Raster-based data in a GIS environment are commonly used to map structure and/or function and investigate change in landscape ecology (Peng et al. 2007). A multitude of landscape metrics (e.g., patch size, patch density, number of edges, edge length, etc) can be calculated from these types of gridded data that help describe the current structure and function of a landscape in addition to gauging how structure and function change over time (Magle et al. 2008). The software packages Fragstats and Patch Analyst are commonly used to calculate these metrics (McGarigal et al. 2002).

Challenges concerning temporal and spatial scales (i.e., both the size/area of a study site and level of detail for the associated data) became particularly evident with the landscape ecology approach because structure, function, and change are scale dependent (Turner 1989). Landscape ecology has the ability to investigate problems at multiple scales (Wiens 1992), but the selected scale of a particular study may drastically alter the conclusions of any study (Turner 1989). These challenges helped to foster the development of new conceptual models for explaining the nested hierarchies of structure, function, and change over multiple scales (Wu & Loucks 1995; Gillson 2004).

Over the last two centuries or so, geographers, botanists, and ecologists have fostered close academic ties and seemed to have developed an appreciation for the inherent strengths of their respective disciplinary perspectives in studying vegetation dynamics. Ample substantiation can be found when considering the founding charter members of the AAG and ESA. One of the most prominent ecologists of all time (Frederick Clements) was an instrumental charter member of the AAG in 1904 and, conversely, a famous geographer (Ellsworth Huntington) played a pivotal role in founding the ESA in 1915 (Cowell & Parker 2003). Additional substantiation can be found when considering that another respected ecologist (Henry Cowles) published the first paper in the Annals (1911), which clearly shared conceptual linkages with a famous geographer's (William Davis) theory of landscape development (Cowell & Parker 2004).

Certainly, disciplinary overlap between geography, botany, and ecology is not a new phenomenon and myriad geographers have made substantive contributions to the ecological literature over the years. Indeed, geographers have historically offered a broader perspective for studying vegetative patterns and processes while thriving at explaining the intertwined linkages between the abiotic and biotic environment; particularly across large spatial extents (Cowell & Parker 2004). Similar work is evident today (e.g., Millward & Kraft 2004) and I intend to continue the spirit of this approach.

CHAPTER III

METHODS

Providing broad and easily comprehensible methodological background information in a manuscript is often challenging, if not impossible, because of the strict journal limitations on page lengths. Conciseness prevails over providing sufficient details in modern academic writing (Graff 2000). Chapter III offers methodological explanations and information that enhances and clarifies some of the methods outlined in the manuscript-based chapters (IV-VI). Section 3.1 discusses aerial photography, Section 3.2 elaborates on the CORONA data and the reconnaissance satellite program that acquired it, Section 3.3 discusses classification schemes and treeline identification, Section 3.4 addresses the DEM and derivations of local site conditions, Section 3.5 addresses geometric corrections for digital imagery, Section 3.6 explores radiometric corrections for remotely sensed images, Section 3.7 discusses the sampling strategy and statistical techniques, and Section 3.8 addresses the calculation of spatial autocorrelation.

3.1 Aerial photography

Contemporary and historical aerial photographs provide invaluable data sources for assessing treeline changes when properly georegistered as a temporal composite of data in a GIS. This section presents supplemental information regarding the aerial photographs that includes and expands beyond information provided in all three of the manuscript-based chapters; including displays of the raw photographs.

3.1.1 Historical photography

Historical aerial photographs can be instrumental in documenting change over extended periods of time, but their coverage is often sporadic, associated metadata are regularly not available, and they commonly are not projected in real-world coordinate systems (Klasner & Fargre 2002). To complicate matters, a plethora of federal agencies such as the USGS, NPS, and USFS in addition to private entities, have collected aerial photographs over the years without a systematic archiving scheme. An exhaustive search was performed for aerial photographs for the study site, but only two potentially suitable selections were found (i.e., those that obviously did not have too much snow or cloud cover, exhibited a fine enough spatial resolution, and were of sufficient quality). The first was a 1:66000 aerial photograph from September, 1955 (Figure 3-1) and the second was a 1:24000 aerial photograph from August, 1969 (Figure 3-2). Additional metadata (beyond the scale, month, and year) were not available for either photograph. After more scrutiny, it was determined that the 1955 photograph was not suitable for quantitative analysis because of patchy cloud cover and dubious image quality near the study site. Thus, the 1955 photography was only used as a qualitative indicator of change.

It is also often problematic to georeference historical aerial photographs because little is known about them in terms of camera specifications, flight altitude, aircraft pitch, aircraft roll, and aircraft type. Because of these uncertainties, unacceptable geometric errors may persist (e.g., RMSE of +/- 12 m) even after instituting georeferencing procedures (Butler et al. 2003). Interestingly, imagery from satellite platforms lacking similar information tend to be more conducive to being georeferenced because orbital paths are much more stable (Jensen 2005). Thus, the 1969 photograph was only used to verify whether any trees existed in the patches of snow on the 1970 CORONA photograph.

3.1.2 Contemporary USGS DOQ

Finding suitable base maps throughout the United States used to be problematic and posed significant challenges to academic researchers and government agencies alike (Davis & Wang 2003). The USGS addressed this issue aggressively in the 1990's with the implementation of a program for generating digital orthophotos. Now, these products are widely disseminated and regularly used as base maps for myriad academic and government mapping/research endeavors; even in remote mountainous areas with treelines (Resler et al. 2004).

According to the USGS (2008), a DOQ is a digital rendition of aerial photography created by a computer in which geometric errors caused by terrain relief and camera tilt have been carefully removed. The original spectral characteristics of the photograph are always maintained through this process. Photographs typically have a spatial resolution of 1 m (sometimes 2 m) and may be panchromatic, black and white, or color-infrared. Full quads are 7.5 minutes longitude by 7.5 minutes latitude, referenced to a NAD27 or NAD83 datum, and cast to a UTM projection. In terms of horizontal accuracy, at least 90% of the test points must be reliable within +/- 40 ft at a scale of 1:24000. DEMs used in the process are also required to have a vertical accuracy of at least +/- 7 m. DOQQs are orthorectified quarter quads (3.75 minutes longitude by 3.75 minutes latitude) that are subjected to equally or more stringent criteria. Remote sensors commonly use DOQs or DOQQs as tie points (e.g., points with known x/y coordinates) when georeferencing images (Davis & Wang 2003). A 2003 DOQQ was used as a base map for tie points and to map areas of tree establishment in this study (Figure 3-3).

3.2 CORONA reconnaissance satellite images

President Clinton (1995) signed an executive order that declassified and released photographic data from the first successful reconnaissance satellite program in the history of the United States. The CORONA program, as it was known, was formally endorsed by President Eisenhower in 1958 (McDonald 1995). The program persevered through eight failures during its seminal stages before finally achieving success on the ninth attempt, which was highlighted by a C-119 making a dramatic mid-air recovery (August 18, 1960) of a capsule embedded with invaluable film for the intelligence community (McDonald 1995). Much of the program targeted the U.S.S.R in an attempt

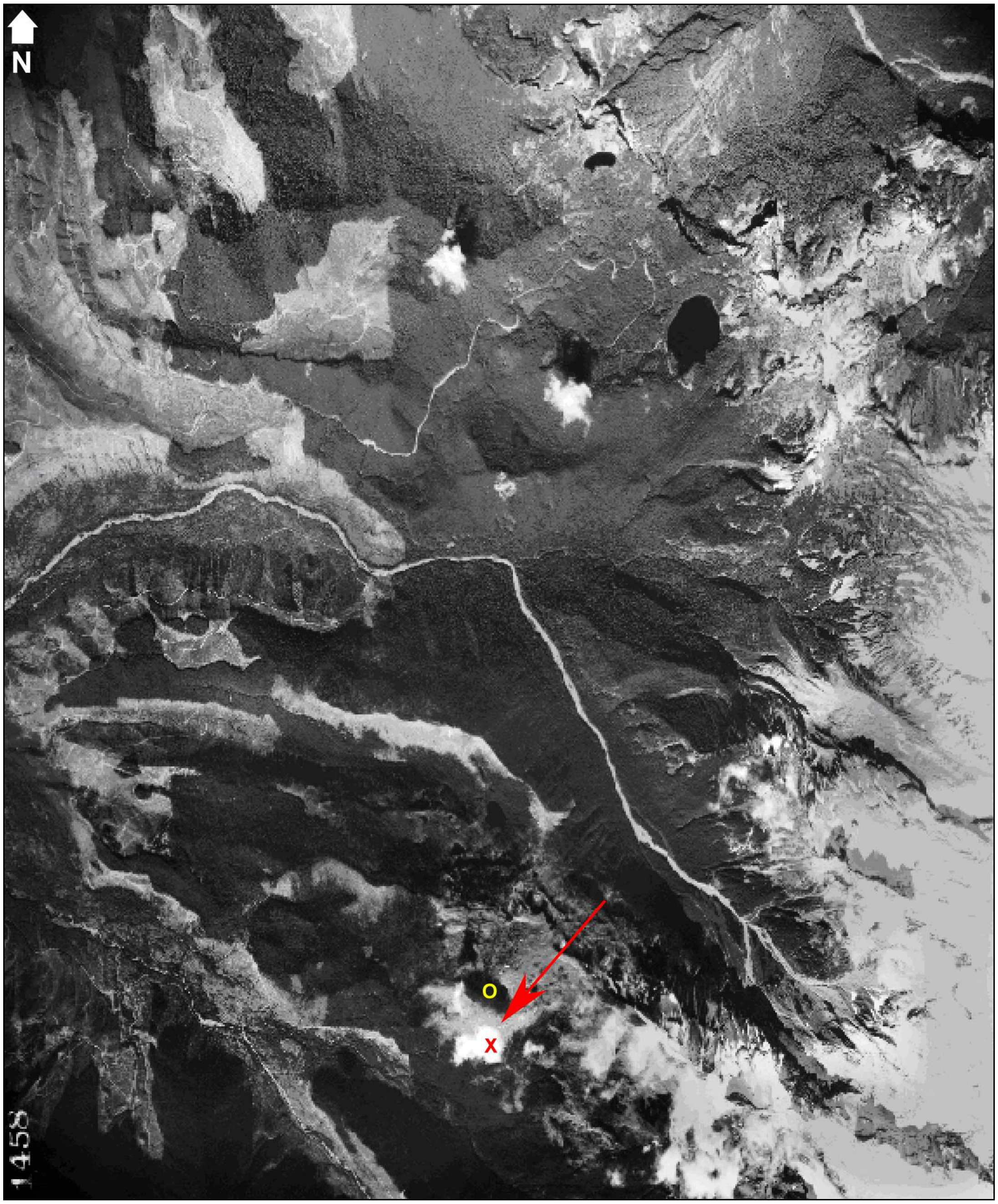


Figure 3-1: A 1955 aerial photograph (~11 km x 19 km displayed above) was used as a qualitative indicator of treeline. The red arrow identifies the ridge that was burned by the 1930 fire. Note how patches of clouds (red X) and shadows (yellow O) conceal portions of treeline that could potentially experience change in future images (Source: USGS).

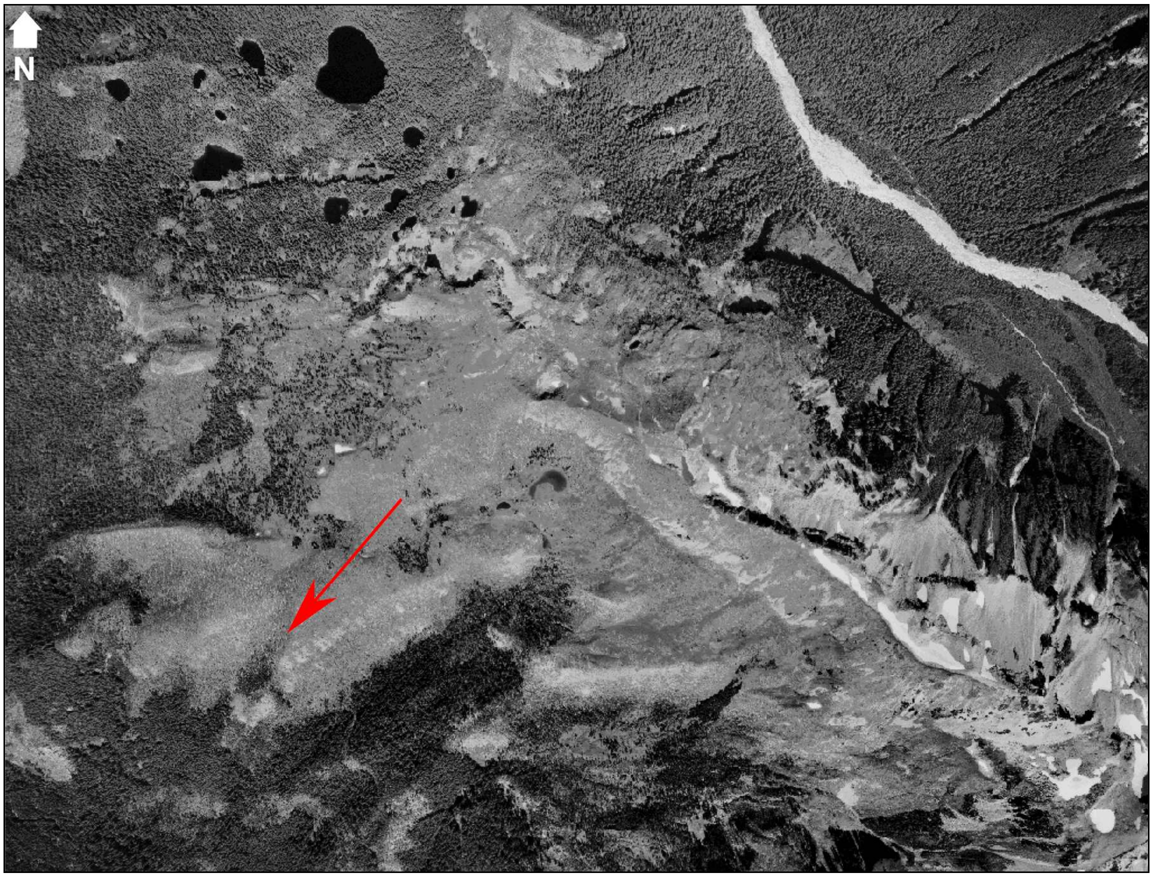


Figure 3-2: A 1969 aerial photograph (~3.5 km x 2.9 km displayed above) was used to verify whether areas blanketed by snow in the CORONA image were occupied by trees. The red arrow identifies the ridge that was burned by the 1930 fire (Source: USGS).

to unveil the Iron Curtain of a very reclusive communist society (McDonald 1995), but large areas of western North America and China were also covered (Andersen 2005). Archived CORONA data covering remote mountainous or otherwise secluded areas often provides some of the earliest baseline aerial or satellite photography for ecological and biogeographic studies (Andersen 2005). Much of this data remains largely unexploited and it could prove to be indispensable in future ecological or biogeographic research (including treelines).

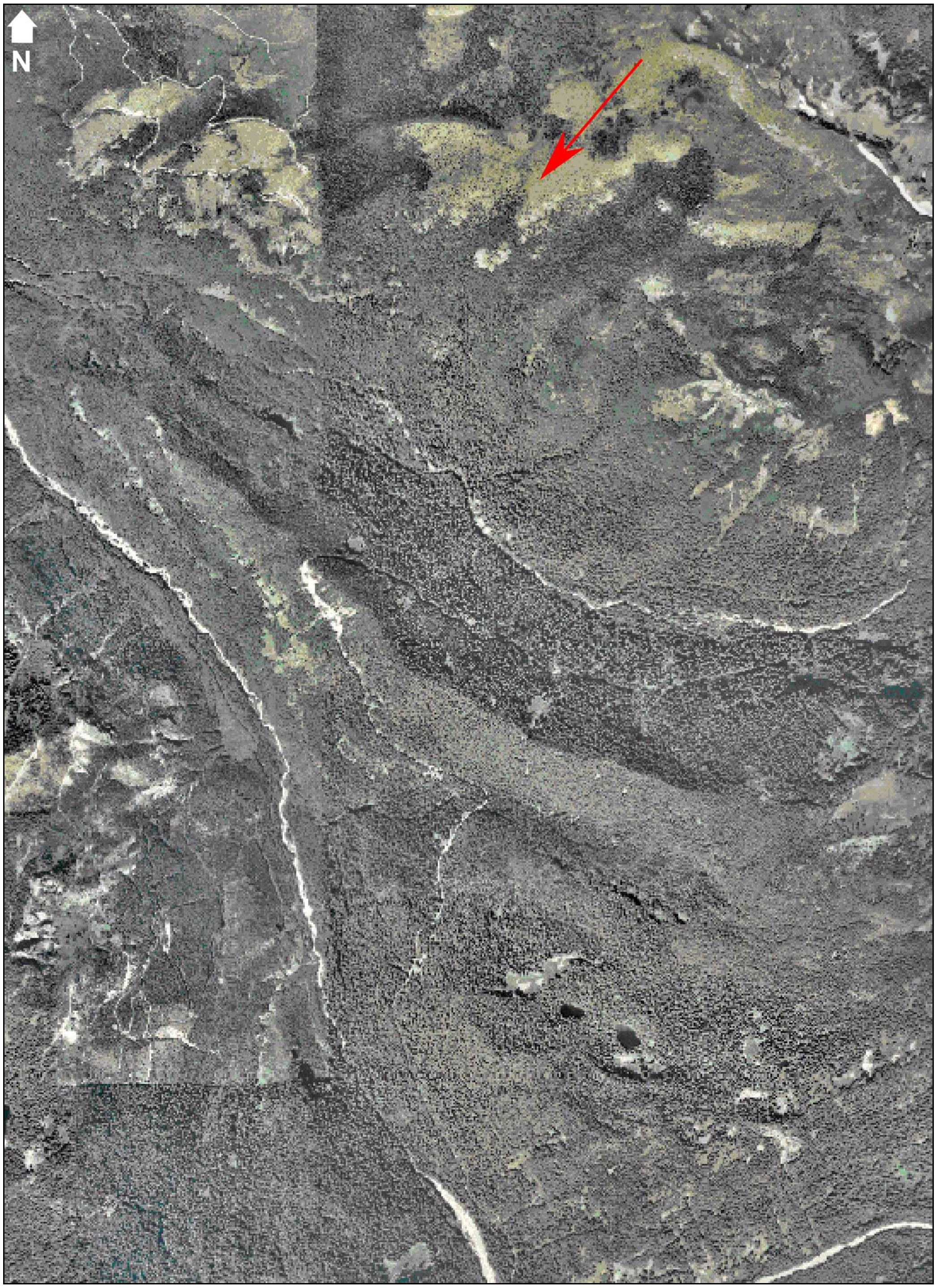


Figure 3-3: A 2003 natural color DOQQ (~4.2 km x 6.1 km displayed above) was used to map trees and collect tie points. The red arrow identifies the ridge that was burned by the 1930 fire (Source: USGS).

Several steadily improved panchromatic camera systems were developed throughout the CORONA program, each referred to by their KEYHOLE (KH) designator (Andersen 2005). Early KH satellites were only able to discern objects that were 15-30 m wide (McDonald 1995). However, some of the highest quality KH satellites were much more advanced. The KH-4B camera system featured an impressive spatial resolution of ~1.9 m at nadir and was the best CORONA satellite (Andersen 2005). Data from the KH-4B system was utilized in this dissertation to assess the distribution of trees in 1970 (I will refer to these trees as '1970 trees' in the remainder of the dissertation).

The KH-4B system contained a dual f/3.5 panoramic camera with a 24-inch focal length and 70 mm film width (McDonald 1995). The camera was specially situated in the satellite so that the forward camera was aft looking and vice versa, thus providing stereo imagery for reliable DEM generation (McDonald 1995; Soun et al. 2004). The KH-4B satellite made orbital passes near 129-150 km and contained supplemental cameras for determinations of pitch, roll, and yaw during operational cycles (McDonald 1995). Relative geometric stability within KH-4B images is strong and generally conducive for use in a GIS if orthorectification procedures are performed (Soun et al. 2004). Specialized orthorectification procedures are necessary if the entire panoramic image (~19.5 x 266.5 km in this case) is to be used; otherwise standard procedures will suffice (Soun et al. 2004). As an additional boon to image quality, polyester-based film was also used in the KH-4B system (as opposed to acetate); greatly diminishing the chances of film either crumbling or jamming during operation (McDonald 1995).

A processed 1970 KH-4B CORONA image was used to map 1970 trees (Figure 3-4). It was selected in favor of the 1969 aerial photograph because of increased platform stability and greater likelihood of acceptable georeferencing procedures.

3.3 Classification procedures, treeline identification, and change detection

Hard classifications are common in treeline studies (e.g., tree, rock, tundra, and water) (Cairns 2001). Hard classification procedures were performed on data that were processed as discussed in 3.5 and 3.6. I used supervised classifications tailored for high spatial resolution panchromatic imagery to delineate trees in 1970 and 2003 (Bai et al. 2005). The green band of the DOQQ was separated for the classification analysis because the signal closely corresponds to the KH-4B panchromatic band.

The green band of the DOQQ was resampled with the nearest neighbor method to match the ~1.9 m spatial resolution of the KH-4B imagery (Jensen 2005). Next, I selected 10 000 training points for each classification category representing trees, shadows (from trees), and treeless areas. I implemented a minimum distance supervised classification with a fitted modal filter to assign shadows to either trees or treeless areas, resulting in a binary classification of trees versus treeless areas (Figure 3-5). Visual estimates from the field and downed boles identified on the 2003 DOQQ indicate treeline used to be much higher (Figure 1-5).

Figure 3-4: Partial strip (panchromatic) of scanned film from the KH-4B CORONA satellite that was used to map trees (~18 km x 13 km displayed above). The tip of the red arrow identifies the ridge burned by the 1930 fire (Source: USGS).

Upper elevations (~1500 m and above) in the KH-4B imagery displayed areas of residual snowpack near some tree patches. I used 1969 aerial photography that was lacking snowpack to verify whether any trees were obscured by snow and the classification was adjusted accordingly.

The 'forest line' was used to determine the lower boundary of treeline and as an easily identifiable reference point for assessing treeline changes in terms of distance and

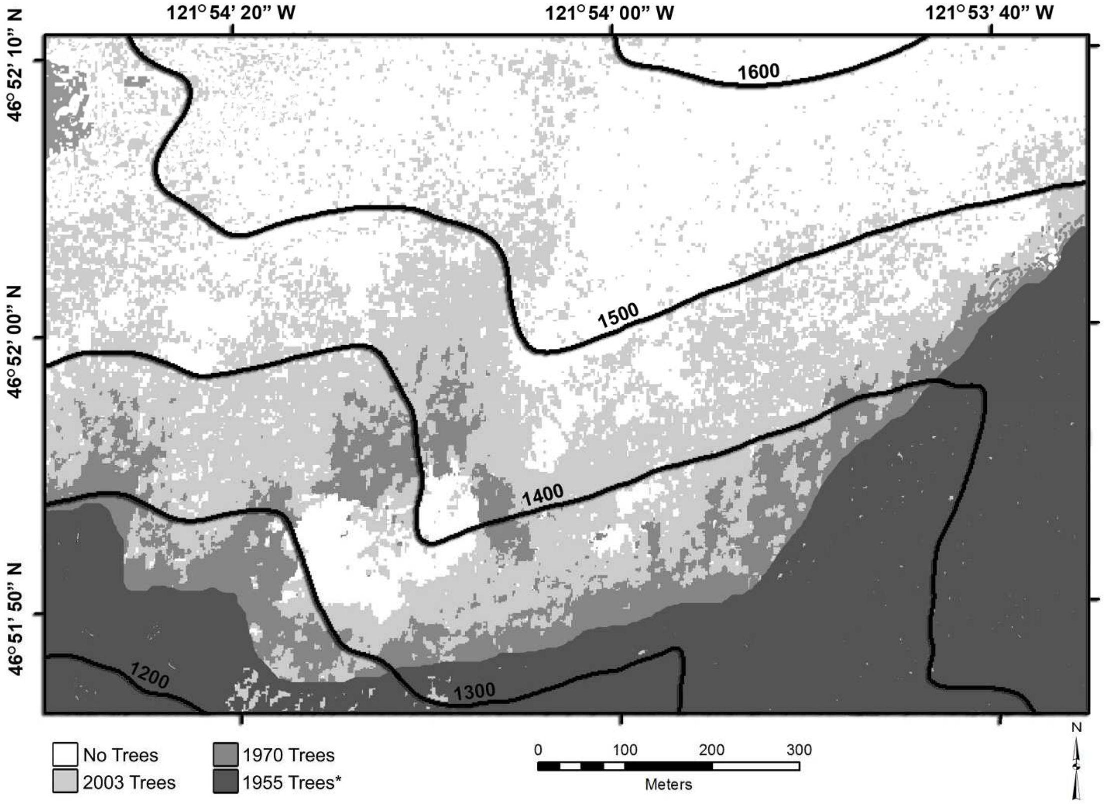


Figure 3-5: The binary classification scheme highlighting a substantial upslope shift in tree establishment at the study site.

elevation (Jobbagy & Jackson 2000) (Figure 1-6). I visually identified and digitized the approximate position of forest line on the 1955 imagery (Figure 3-5). Forest line in the classified 1970 satellite imagery and 2003 aerial photography was identified by using a GIS to detect the highest altitudinal limits of pixels classified as trees that were contiguously connected to closed forest. I quantified maximum and minimum forest line changes in a GIS by assessing upslope measurements from each pixel in the 1970 forest line that were perpendicular to slope contours. Treeline was defined as all pixels 30 m below the 1970 forest line and continuing to the highest elevations attained by pixels classified as trees in the 2003 aerial photography for inclusion in the landscape metrics and statistical analyses. Lastly, change detection was performed to identify areas of establishment at treeline between 1970 and 2003.

3.4 Digital elevation data

Digital representations of topographic features are regularly utilized when studying treeline ecosystems to quantify a plethora of environmental variables such as elevation, slope aspect, slope angle, and related wetness or snow indices (Brown 1994b). These variables are markedly important in treeline environments because they appear to exert a significant amount of influence on both pattern and process in arboreal vegetation (Cairns 2001). In the past, 10- or 30-m USGS DEMs were commonly used for these purposes (e.g., Brown 1994b). However, viable alternatives, such as DEMs produced from LIDAR are being more commonly used.

3.4.1 LIDAR

LIDAR employs the use of an airborne laser rangefinder that successively scans an area of interest and records elevation values for the eventual production of high-spatial-resolution DEMs (Jensen 2005). The Puget Sound LIDAR Consortium (2008) specializes in public-domain data for western Washington and supplied access to a LIDAR-generated DEM (1.8 m) for the study site. They provided access to bare earth surface data that was acquired by a joint venture between NASA and the USGS. Terrapoint (2003) was contracted by these two agencies to collect the data. In general, the quality of the data is vastly superior to the best USGS DEMs. Vertical accuracy is often within +/- 1 ft, but may be worse in areas with heavy timber (e.g., the dense old-growth montane forest). The data is also suitable for 1:12000 scale mapping specifications.

3.4.2 Preprocessing procedures

The acquired 1.8-m LIDAR-based DEM was already partially processed and a 'bare-earth' model was made available on the Puget Sound LIDAR Consortium website. Vegetation peaks (e.g., tree tops) were removed (e.g., Keqi et al. 2003; Rottensteiner et al. 2005), geometric corrections were applied, and the data were properly projected in space. As a precautionary measure to confirm the reliability of the LIDAR-based DEM, elevation values derived from it were visually compared with a corresponding 10-m USGS DEM in a GIS environment and generally found to be consistent. However, it was noted that it provided more detailed topographic information that often varied between cells in the USGS DEM. For example, 10-m cells with specified elevation values often had several corresponding LIDAR-based values that were +/- 0.5 m of the original 10-m elevation value. I applied a series of 5x5 smoothing filters to remove systematic speckling that was apparent in the data and eliminate any rogue tree tops that may have survived the tree removal algorithms (Figure 3-6).

3.4.3 Deriving local site conditions

Data for a suite of variables thought to influence establishment patterns were obtained from the LIDAR-based DEM, ancillary climate data, and mapped areas of trees (see section 3.3) (Franklin et al. 1971; Henderson 1974; Agee & Smith 1984; Shankman 1984; Rochefort & Peterson 1996). Elevation values were extracted directly from the DEM (Figure 3-7). I calculated slope aspect and slope angle with a 3x3 window while considering all eight surrounding pixels (Burrough & McDonnell 1998) (Figure 3-7). I calculated snow index values from curvature (Zevenbergen & Thorne 1987; Moore et al. 1991), southwesterly prevailing winds, elevation, slope aspect, and slope angle (Frank 1988; Burke et al. 1989; Brown 1994b) (Figure 3-8). Topographic concavities and leeward slope aspects at high elevations were weighted with the highest snow potential

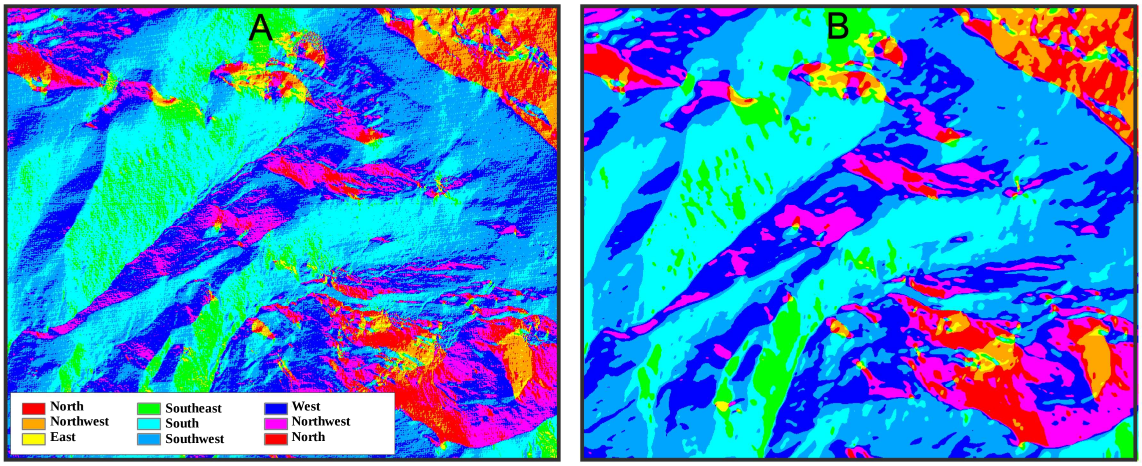


Figure 3-6: Slope aspect derived from the LIDAR-based surface DEM using 8 surrounding pixels. Image A was based off the raw data and image B was treated with a smoothing filter.

(i.e., more likely to have deep season-shortening snowpack from wind-driven snow deposits). I calculated wetness index values from the upslope catchment area and drainage patterns quantified in the DEM (Beven & Kirkby 1979; Brown 1994b) (Figure 3-8). Enclosed depressions with large upslope moisture catchment areas were weighted with the highest wetness potential (i.e., likely to have moist and cool soils). I determined the sediment erosion index values by considering calculations of slope angle and flow accumulation from the DEM (Moore et al. 1993) (Figure 3-8). Steep convex landscape features and open concavities with large upslope moisture catchment areas (e.g., ravines and stream beds) were weighted with the highest erosion potential (i.e., surfaces likely to be regularly disturbed by erosion forces). Proximity to and direction from trees 1970 trees was calculated with standard Euclidean distance measures using the 1970 trees as source areas (Figure 3-9).

3.5 Geometric processing

When digital information or maps are utilized in a GIS environment, it is absolutely crucial to consider the geometric accuracy of the data (Jensen 2005). Ideally, all digital data would be properly manipulated and formatted so that it aligns or ‘stacks’ properly over data from a similar location in a standard map projection (Figure 3-10). Under such circumstances, x/y coordinates collected from one digital data set should correspond with similar points on another overlaying data set. Unfortunately, some of the most valuable digital data sets for treeline studies (e.g., historical aerial photography

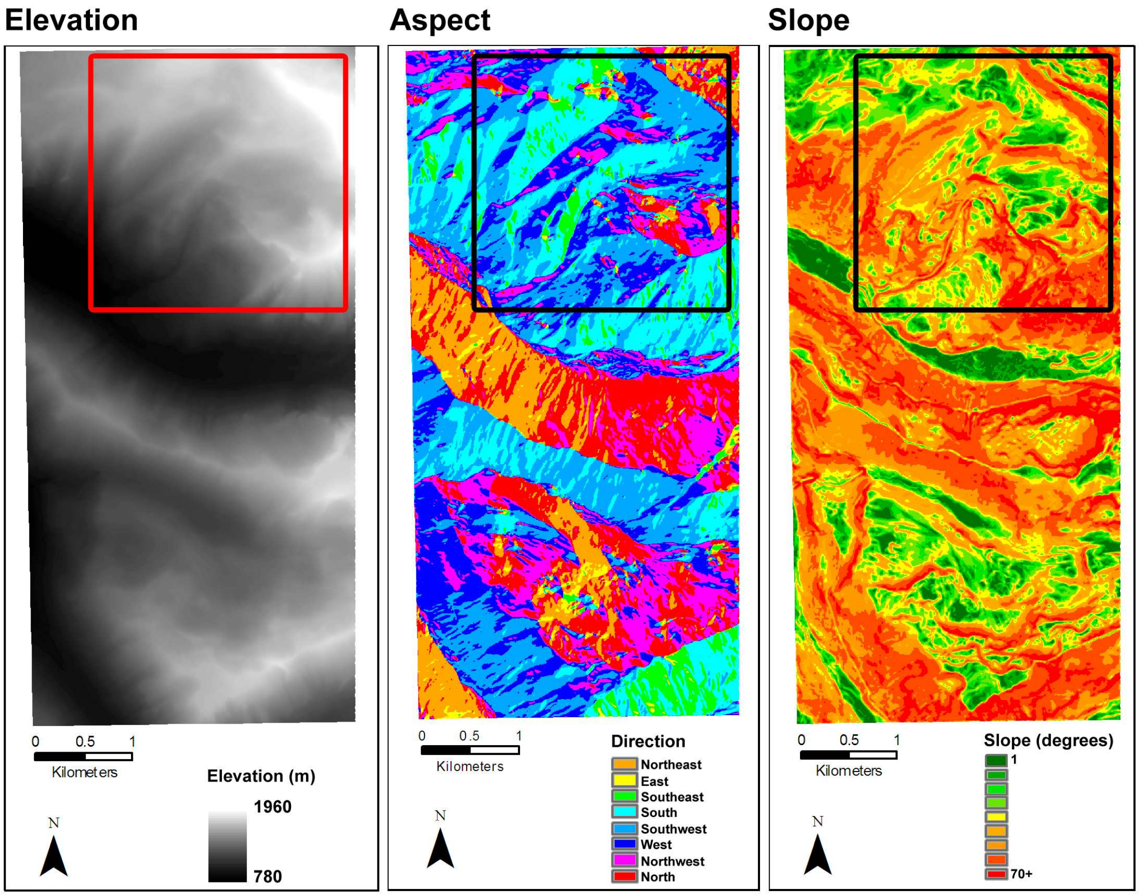


Figure 3-7: Standard variables extracted or derived from the LIDAR-based DEM. In this figure, these include elevation, slope aspect, and slope angle. The red and black squares respectively highlight the area containing the study site. All eight surrounding pixels were considered when determining what slope aspect and slope angle values to assign to respective pixels.

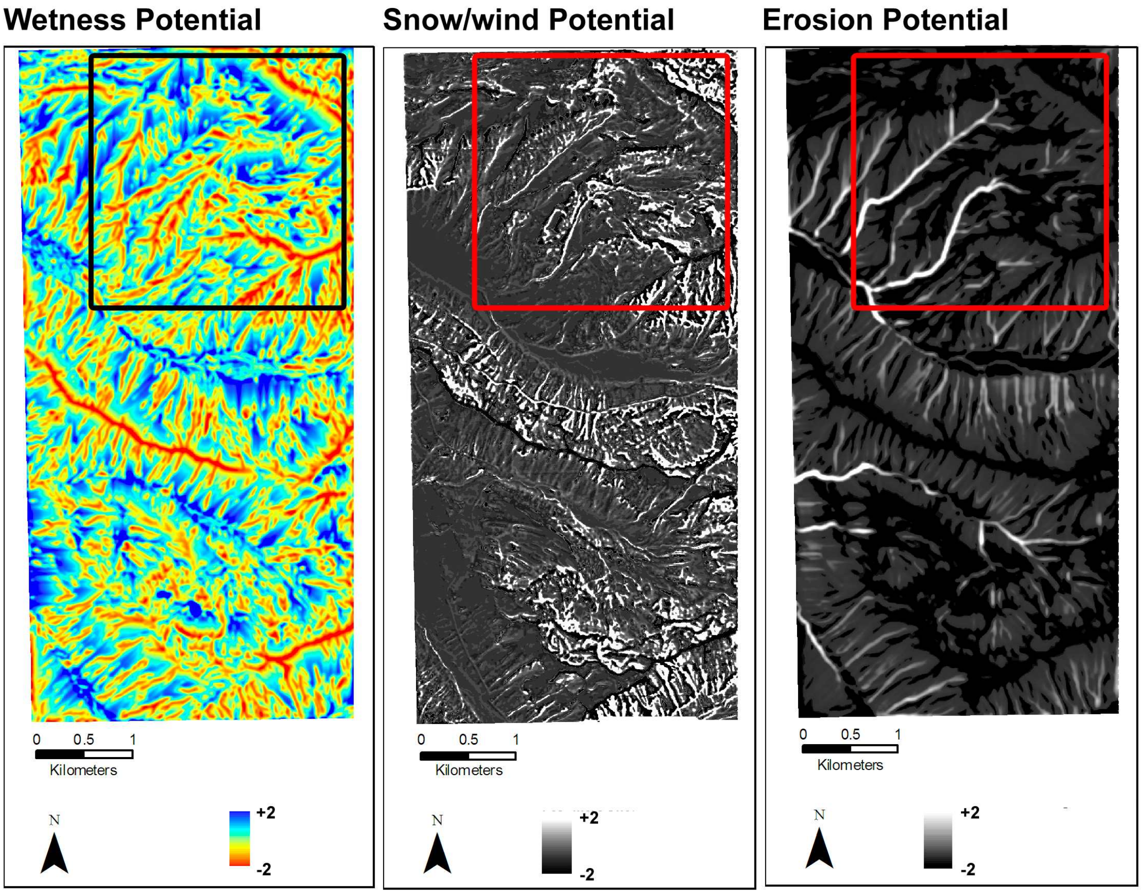


Figure 3-8: Non-standard variables derived from the LIDAR-based DEM and the prevailing wind direction. In this figure, these are wetness, snow/wind, and erosion. The red and black squares respectively highlight the area containing the study site. Values have been scaled to between 2 and -2. Positive values indicate the likelihood of wetter, snowier (less wind), and more erosive conditions respectively. Negative values indicate the likelihood of drier, windier (less snow), and less erosive conditions respectively.

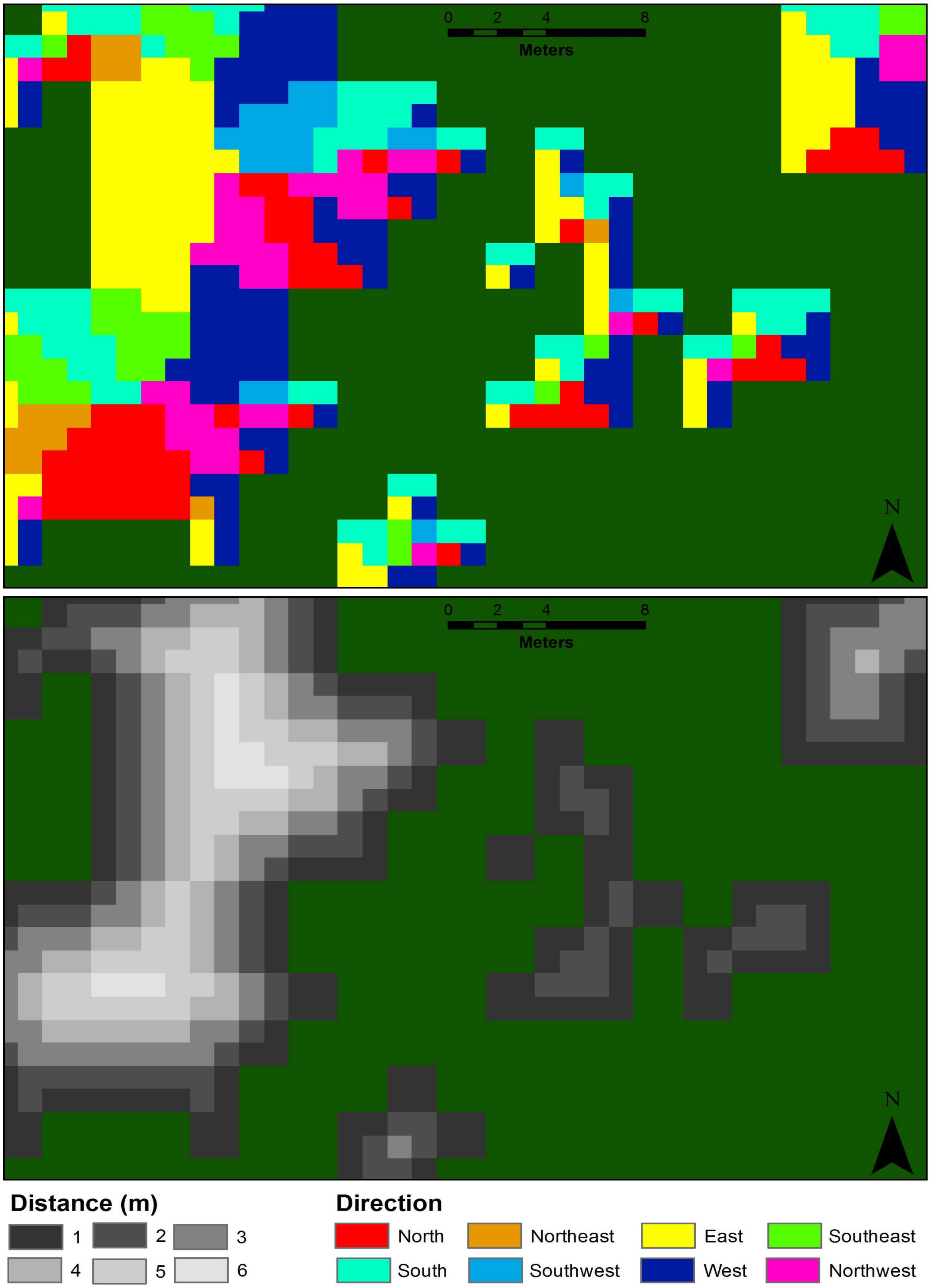


Figure 3-9: Raster-based example denoting 'proximity to 1970 trees' (bottom) and 'direction from 1970 trees' (top). The 1970 trees are denoted by dark green pixels.

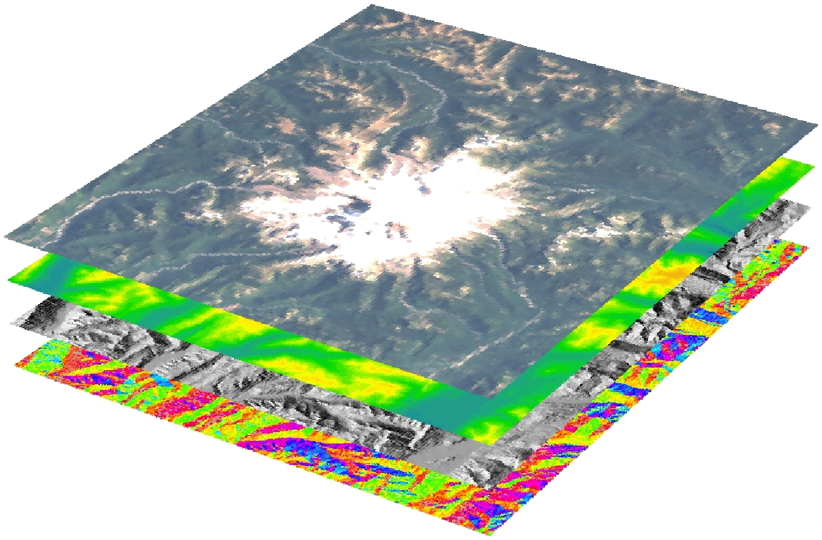


Figure 3-10: A spatial composite of digital data from Mount Rainier and the surrounding landscape properly georeferenced and stacked in a GIS environment (Source: USGS and Global Land Cover Facility).

or CORONA satellite imagery) have not been properly cast in real-world coordinates. Geometric corrections must be instituted in these cases for proper use in a GIS. These challenges have inhibited and in some cases prevented biogeographers and ecologists from exploiting the use of historical remotely sensed data in their research. However, processing software that is increasingly user friendly is allowing some historical data to be accessed and properly processed (Jensen 2005).

3.5.1 Standard georeferencing

Standard geometric correction involves aligning points of known real-world coordinates (e.g., tie points or GCPs) with uncorrected digital data and implementing mathematical equations (usually 1st order polynomial) to calculate real world coordinates for the uncorrected data (Jensen 2005):

1st order polynomial: $x' = Ax + By + C$

$y' = Dx + Ey + F$

where x is the column count in an unprojected image, y is the row count in an unprojected image, x’ is the horizontal value in an projected image, y’ is vertical value in an projected image, A is the width of a raster cell, B is a column term for rotation, C is the x’ value of the center of the cell in the upper right corner, D is a row term for rotation, E is the negative height of a raster cell, and F is the y’ value of the center of the cell in the upper right corner. Sometimes a 2nd order polynomial or high transformation is necessary in rugged terrain. It is recommend to select at least 18 widely distributed GCPs from easily identifiable points (e.g., road intersections, trails, etc) and to concentrate several of the points throughout the perimeter of the image (Jensen 2005). Perfect image alignment never occurs and the RMSE is used to quantify any residual image distortion:

$$\text{RMS}_{\text{error}} = \sqrt{(x'-x)^2 + (y'-y)^2}$$

where x and y are the original row and column coordinates of the tie point and x’ and y’ are the calculated coordinates. Widely accepted scientific criterion for adequate geometric correction procedures typically require RMSE values at or below 0.5 (e.g., Stueve et al. 2007). Unfortunately, standard geometric corrections do not properly correct or mitigate geometric displacement caused by topographic variability, remote sensing platform variability (e.g., pitch, roll, and yaw), and camera/sensor specifications.

Such errors (especially those related to topography) are typically quite severe in mountainous terrain and require more advanced treatment in order to maintain confidence in the geometric accuracy of the data (e.g., Butler et al. 2003).

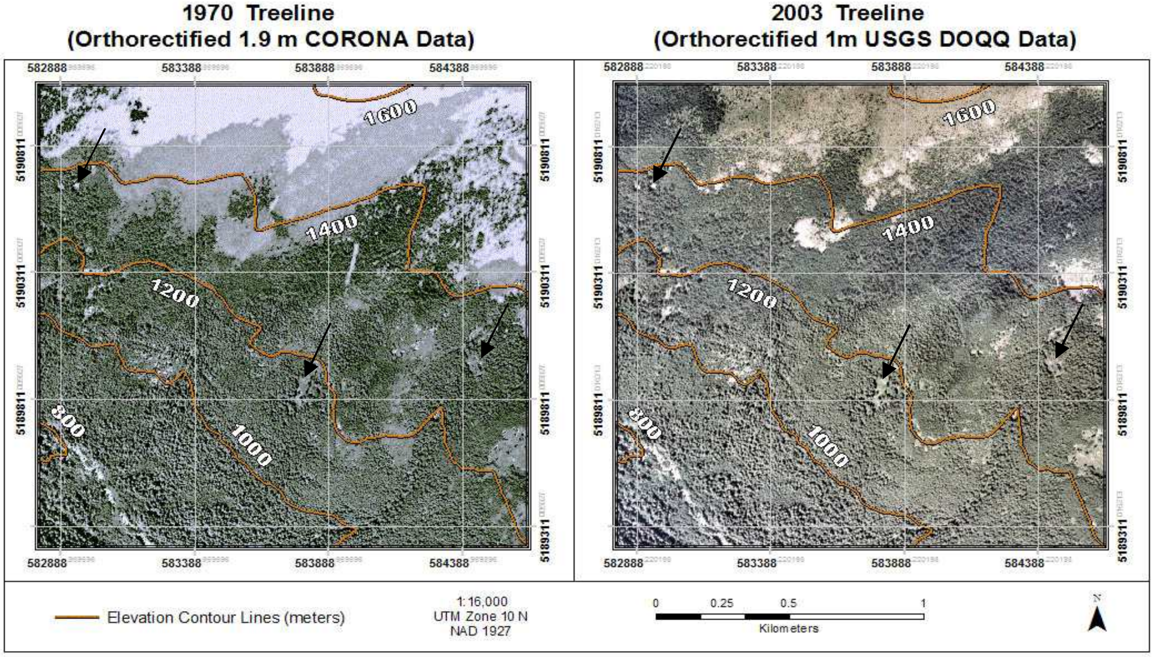
3.5.2 Orthorectification

Orthorectification is a more complex procedure that mitigates geometric displacement stemming from topography, remote sensing platform variability, and camera/sensor specifications. Modeling the influence of topography is especially crucial in mountainous terrain and necessitates the use of a corresponding high-quality DEM (e.g., Stueve et al. 2009). Similar to the standard method, tie points are carefully selected throughout the image from easily identifiable points of known real-world coordinates. However, the DEM is also used in concert with the tie points and estimated altitudinal or orbital position of the remote sensing platform to mathematically model geometric displacement caused by topographic variability (Jensen 2005).

CORONA KH-4B photography from mission 1110 on June 2 of 1970 was subjected to orthorectification procedures. A parametric model was used with the nearest neighbor resampling in concert with direct linear transformation and bundle adjustment to build the exterior orientation (Fiore 2001; Toutin 2002). The 1-m 2003 USGS DOQQ served as the base aerial photography for the collection of 42 ground control points that were evenly distributed throughout the photography with an RMSE of 0.495 (Davis & Wang 2003). The LIDAR-based 1.8-m DEM (Terrapoint 2003) and KH-4B satellite specifications from declassified documents (McDonald 1995) were used to model the terrain and satellite position during orthorectification. The resultant orthorectified image aligned quite well with the 2003 aerial photograph (Figure 3-11)

3.6 Radiometric processing

Inconsistent or misleading data from radiometric variability may surface from a variety of sources in remotely sensed images from the visible to near-infrared portions of the electromagnetic spectrum. Sensor failures leading to striping, line drop-outs, or some other phenomena can occur sporadically, but the influences of atmospheric scattering and variable illumination geometry on electromagnetic reflectance tend to have more serious consequences in terms of data analysis and interpretation (Jensen 2005). Atmospheric correction algorithms (e.g., dark subtraction and empirical line calibration) and normalizations of sensor illumination (e.g., at-satellite reflectance) are usually only required when biophysical assessments of vegetation over time are being made (e.g., vegetation vigor as determined, for example, by NDVI) (Stueve et al. 2007). However, shadows from topographic variability (topographic effect) can be problematic in mountainous terrain. Here, it may be necessary to use training areas at disparate topographic positions, band ratioing techniques, and topographic correction models to



1970 Treeline
(Orthorectified 1.9 m CORONA Data)

2003 Treeline
(Orthorectified 1m USGS DOQQ Data)

Figure 3-11: Orthorectified 1970 CORONA photograph (left) visible as a transformed color composite and the orthorectified 2003 DOQQ on the right. The currently displayed spatial extent was chosen so that several landscape features common between both photographs (upper and lower elevations) can be visually identified and compared (highlighted by arrows). Visual confirmation indicates the alignment between the photographs is excellent (Source: USGS).

mitigate the effect of shadows (Blesius & Weirich 2005). The Minnaert correction is a common approach that utilizes a corresponding DEM and estimated sun/sensor geometries in mitigating the topographic effect (Itten & Meyer 1993; Blesius & Weirich 2005). The Minnaert correction was performed on the photographs, but there was little difference between the before/after images. As is evident in figure 3-11, the broad south-facing slopes of the ridge were illuminated quite well; which probably made this correction unnecessary.

3.7 Sampling strategy and statistical techniques

Sampling strategies, correlated independent variables, and the type of multivariate statistical technique employed can all influence the results of a statistical analysis; and possibly make the results questionable, depending upon the care and reasoning used in the analysis (Whittingham et al. 2006). Important statistical steps and the rationale are highlighted below.

3.7.1 Stratified random sampling

I generated 1000 points in a stratified random sampling scheme that began just below the '1970 forest line' and extended up to the uppermost limits of trees in the 2003 aerial photograph (Figure 3-12). The purposes of selecting 1000 randomly sample points in a stratified scheme were to mitigate the effects of spatial autocorrelation and to maintain enough points to ensure statistical rigor with the logistic regressions. Commonly, as few as 80 points are used in logistic regressions with a high amount of confidence when using eight independent variables (Hosmer & Lemeshow 2000). However, I selected 1000 points because of the wide ranges observed in the data of the local site conditions (e.g., to ensure that at least 10 points were available at the extremes of the dataset).

3.7.2 Pearson's correlation and multicollinearity

Pearson's correlation test is a classic measure of linear correlation between variables that is widely used in biogeography (e.g., Berendse et al. 2001):

$$r = \frac{\sum_{i-1}^{n}\left(X_i - \overline{X}\right)\left(Y_i - \overline{Y}\right)}{(n-1)S_X S_Y}$$

where X and Y are independent variables with corresponding means $\left(\overline{X}, \overline{Y}\right)$ and

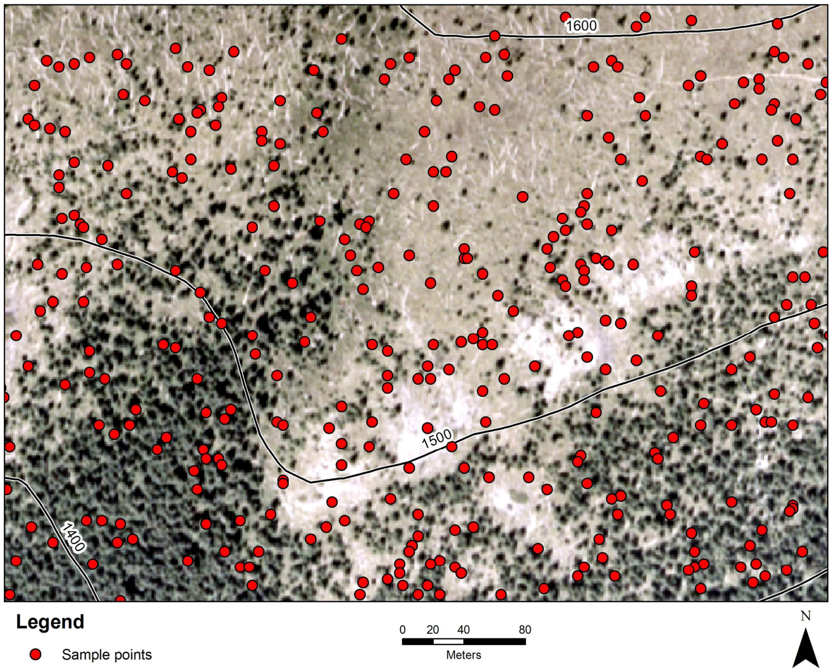


Figure 3-12: A snapshot of 334 sample points at treeline with the 2003 aerial photograph in the background.

standard deviations (S_X, S_Y). This test is commonly applied before performing logistic regression to determine if there is multicollinearity among the independent variables that may compromise results. It is inappropriate to use traditional stepwise logistic regression if specific Pearson’s correlation thresholds are exceeded. Hosmer and Lemeshow (2000) recommend that no two independent variables exceed the 0.7 threshold, but others (e.g., Hessl & Baker 1997) consider 0.5 to be overly correlated. Independent variables were subjected to Pearson’s correlation test to examine the data for multicollinearity. Several variables were strongly correlated when extracting a stratified random sample of 250 points (Table 3-1).

3.7.3 Traditional logistic regression (forward and backward)

I used SPSS v.12.0.1 for Windows (2004) to perform traditional binomial stepwise logistic regression and test the null hypothesis that tree establishment patterns were not related to local site conditions. I selected this approach because it is widely used, the dependent variable is dichotomous, and it has less stringent assumptions in terms of normally distributed variables, homoscedasticity, and linearity between the dependent and independent variables (Hosmer & Lemeshow 2000). Both backward (variables removed one at a time) and forward (variables added one at a time) logistic regression were used to analyze the data and determine what independent variables were most important in controlling tree establishment patterns. I chose to implement both because they have been known to provide contradictory rankings and having consistent results between both approaches lends more credence to the rankings (Kupfer et al. 2008). The following equation describes the basic logistic regression approach:

$$Y = \ln [p / (1-p)] = ß_0 + (ß_1X_2) + (ß_2X_2) + (ß_3X_3)\ldots(ß_nX_n)$$

where ln is the natural logarithm, p is the probability of obtaining a positive response, $ß_{0,}$ $ß_{1,}$ $ß_{2,\ldots}ß_n$ are parameters estimated from observed data, and X_1, X_2, X_3,…, X_n are independent variables. The potential inclusion of variables at each step was determined using the stepwise likelihood ratio method with a level of *P* = 0.05 for entry and *P* = 0.10 for removal.

Scatterplots were assessed to determine whether independent variables were related linearly to the logit of the dependent variable. The square root, quadratic, and logarithmic transformations were used to diminish the effects of nonlinearity and also to lower skewness and kurtosis values near 0.5. The Wald statistic was used to rank the importance of independent variables (Agresti 1996). This statistic tests the significance of the model coefficient and is calculated by dividing the model coefficient by the corresponding standard error and squaring the result. The Wald statistic is superior to the beta coefficient in identifying important independent variables because it is not as susceptible to extreme values in the independent or dependent data (Cumming 2000). The most important independent variables correspond with larger Wald values.

3.7.4 Logistic regression in the hierarchical partitioning framework

Chevan and Sutherland (1991) discussed a logistic regression method based on the mathematical hierarchical theorem. Later, Mac Nally (1996, 2000, 2002) promoted

Table 3-1: Resulting Pearson correlation coefficients (top line of each pair) and significance values (bottom line of each pair) between the independent variables used in the regression analyses. According to some scholars, correlations beyond 0.7 are strong and capable of introducing errors into traditional regressions. Others argue that those beyond 0.5 are too strong.

	Elevation	**Proximity to 1970 Trees**	**Direction from 1970 Trees**	**Slope Aspect**	**Slope Angle**	**Snow Potential**	**Erosion Potential**	**Wetness Potential**
Elevation	1	------	------	------	------	------	------	------
	0.000	------	------	------	------	------	------	------
Proximity to 1970 Trees	0.696	1	------	------	------	------	------	------
	0.000	0.000	------	------	------	------	------	------
Direction from 1970 Trees	0.207	0.261	1	------	------	------	------	------
	0.000	0.000	0.000	------	------	------	------	------
Slope Aspect	0.224	0.280	0.358	1	------	------	------	------
	0.000	0.000	0.000	0.000	------	------	------	------
Slope Angle	-0.408	-0.468	0.019	0.122	1	------	------	------
	0.000	0.000	0.275	0.000	0.000	------	------	------
Snow Potential	-0.216	-0.196	0.129	0.017	0.194	1	------	------
	0.000	0.000	0.000	0.295	0.000	0.000	------	------
Erosion Potential	-0.139	-0.098	0.344	0.248	0.318	0.424	1	------
	0.000	0.001	0.000	0.000	0.000	0.000	0.000	------
Wetness Potential	0.107	0.219	0.287	0.173	-0.204	0.289	0.666	1
	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

the potential contributions of such an approach in ecological research and introduced it in the statistical package *R*. Hierarchical partitioning calculates incremental improvements of traditional regression models by incorporating a given variable and averaging its effects throughout all possible combinations with other variables (Mac

Nally 1996). For example, consider the effects of some independent variable (*A*) on all first-order, second-order, third-order, and higher-order models (as discussed by Mac Nally 1996). If *A* has a significant independent influence, model fits for any of the first- and higher-order models will be better when *A* is included. In hierarchical partitioning, all variables in regression models are thoroughly and consistently assessed in this manner. Such an approach has been posited to mitigate the effects of multicollinearity and provide a more reliable ranking of independent variables (Mac Nally 1996).

I executed this approach on the transformed data (i.e., from the traditional logistic regression section) using *R 2.4.1* (2006) to test the null hypothesis that tree establishment patterns were not related to local site conditions. The randomization method was also employed to calculate Z-values and gauge whether or not each of the respective independent variables were statistically significant (Mac Nally 2002).

3.8 Modeling spatial autocorrelation

Failure to account for spatial autocorrelation can confound statistical analyses of ecological phenomena and may result in the erroneous identification of important independent variables and their relative rankings (Griffith & Peres-Neto 2006). To address spatial autocorrelation, I used *R 2.4.1* (2006) to implement a modification of the principal coordinates of neighbour matrices approach based on eigenvectors and distance (Dray et al. 2006). I selected the Delaunay triangulation to generate the spatial weights matrix based off data-driven Akaike information criterion rankings. The weighted matrix is an indicator of the spatial relationship between the sample points. Boris Delaunay (1934) invented the triangulation, which tries to form a circumcircle of a triangle from three points that do not contain intersecting vertices beyond the points used to create it (Figure 3-13). Results consisted of positive (i.e., similar neighbors clustered in space) and negative (i.e., dissimilar neighbors) eigenvalues in continuous data formats that corresponded well with the traditional Moran's I measure of spatial autocorrelation. I included the data as an additional independent variable in the regression analyses (Griffith & Peres-Neto 2006).

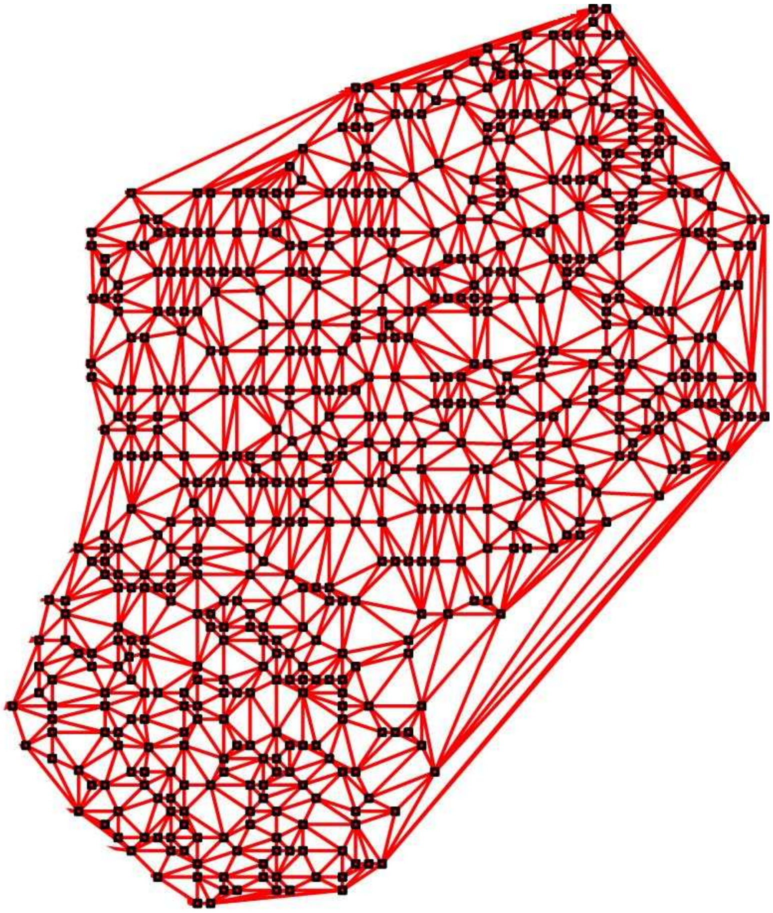


Figure 3-13: An example of the Delaunay triangulation calculated from a random sample of 500 points at the study site.

3.9 Ground verification and accuracy assessments

Field verification of changes identified from remotely sensed data is necessary to bolster the degree of confidence in the resulting classifications and analyses (e.g., Stueve et al. 2007). A crucial consideration for verifying the images are the number of ground truth points obtained from the field that should be incorporated in the assessment. Fitzpatrick-Lins' binomial probability theory was utilized for this study (c.f. Jensen, 2005). It suggests approximately 80 ground verification points should be acquired from the study site. I marked 60 ground verification points with a WAAS corrected global positioning system and 23 additional points with an uncorrected global positioning system (due to obstructions from large trees). Visual confirmation of relatively stable points of rock and 'old' trees were identified in the field (26 patches of rock and 23 patches of 'old' trees). Additionally, 15 tree ring cores and 19 cross sections were collected from widely distributed areas identified as experiencing tree establishment on photography. I subjected the tree ring simples to standard processing before counting the tree rings and determining tree ages (Fritts & Swetnam 1989).

I used the verification points to assess the accuracy of three different classifications including minimum distance, maximum likelihood, and isodata (Table 3-2). The first two are supervised classifications and the latter is an unsupervised classification. Minimum distance provided superior results and thus I used this approach in all classification procedures (discussed in 3.3).

Table 3-2: Classification accuracies for three different approaches.

1970 CORONA Supervised Minimum Distance Classification

			Total	Omissions	Commissions	Map Accuracy
	Trees	Treeless				
Trees	34	2	36	5.6%	19.4%	79.1%
Treeless	7	40	47	14.9%	4.3%	81.6%
Total	41	42	83			
	Overall Classification Accuracy =		89.2%			

2003 DOQQ Supervised Minimum Distance Classification

			Total	Omissions	Commissions	Map Accuracy
	Trees	Treeless				
Trees	57	3	60	5.0%	6.7%	89.1%
Treeless	4	19	23	17.4%	13.0%	73.1%
Total	61	22	83			
	Overall Classification Accuracy =		91.6%			

1970 CORONA Supervised Maximum Likelihood Classification

			Total	Omissions	Commissions	Map Accuracy
	Trees	Treeless				
Trees	23	13	36	36.1%	27.8%	50.0%
Treeless	10	37	47	21.3%	27.7%	61.7%
Total	33	50	83			
	Overall Classification Accuracy =		72.3%			

2003 DOQQ Supervised Maximum Likelihood Classification

			Total	Omissions	Commissions	Map Accuracy
	Trees	Treeless				
Trees	45	15	60	25.0%	16.7%	64.3%
Treeless	10	13	23	43.5%	65.2%	34.2%
Total	55	28	83			
	Overall Classification Accuracy =		69.9%			

1970 CORONA Unsupervised Isodata Classification

			Total	Omissions	Commissions	Map Accuracy
	Trees	Treeless				
Trees	24	12	36	33.3%	25.0%	53.3%
Treeless	9	38	47	19.1%	25.5%	64.4%
Total	33	50	83			
	Overall Classification Accuracy =		74.7%			

2003 DOQQ Unsupervised Isodata Classification

			Total	Omissions	Commissions	Map Accuracy
	Trees	Treeless				
Trees	46	14	60	23.3%	20.0%	63.9%
Treeless	12	11	23	52.2%	60.9%	29.7%
Total	58	25	83			
	Overall Classification Accuracy =		68.7%			

All three approaches produced somewhat reasonable results, which most likely can be attributed to the relatively small spatial extent of the study area and high spectral contrast between the subalpine forest and alpine tundra (Bai et al. 2005). Maximum likelihood and isodata often produce better results, but these approaches also assume that the spectral response of each class is Gaussian (Jensen 2005). In this case, the spectral responses of the classes exhibited some skewness (3-8) and kurtosis (6-9), which probably explains why the nonparametric minimum distance approach was superior.

CHAPTER IV

ASSESSING POST-FIRE TREE ESTABLISHMENT AT ALPINE TREELINE: A HIERARCHICAL PARTITIONING APPROACH

4.1 Introduction

Alpine treeline (treeline) is the transition zone or ecotone between closed forest and open alpine tundra. It represents the uppermost altitudinal limit attained by trees in mountainous regions (Resler 2006). The structural and compositional characteristics of treeline vary widely across the globe (Holtmeier 2003). The transition may be abrupt (e.g., 10 m or less) or gradual (e.g., 100 m or more) and may or may not include krummholz (Holtmeier 2003). When krummholz is present, it may persist as a climatically-stunted, asymmetrical form of upright arboreal species found below treeline or as an entirely different genetically-determined species of tree (e.g., *Pinus mugo prostrate* and *Alnus viridis*) (Holtmeier 1981). In some cases, treeline may span several hundred meters of a patchy mosaic of arboreal (both upright and krummholz forms) and herbaceous vegetation, such as the subalpine parkland common throughout the Pacific Northwest (Stueve et al. 2009).

Treeline is one of the most conspicuous landscapes in the world and has been observed and/or studied for over 200 years in the literature (e.g., von Humboldt 1807; Greene 1872; Wilcox 1899; Jobe 1915; Griggs 1938; Daubenmire 1954; Tranquillini 1979; Warlde 1985; Kullman 1987; Brown 1994b; Butler et al. 1994; Malanson 1997;

Holtmeier 2003; Cairns & Moen 2004; Camarero & Gutiérrez 2004; Resler et al. 2005, Stueve et al. 2009). Many of the earliest references to treeline (early 20th century and before) mostly noted its presence during mapping activities or geographical exploration. Other studies dating from the 19th to mid-20th centuries were more scientific and aimed to explain the presence of treeline at specific elevations (c.f. Körner 1998). Temperature was posited to control treeline elevations in many of these studies (e.g., treeline seemed to correspond to mean air temperature of about 10°C in the warmest month) (c.f. Körner 1998). Accordingly, several scholars later hypothesized that treeline may serve as a useful indicator of climate change (e.g., Kullman 1995; Grace et al. 2002). Others remained skeptical, asserting that multiple abiotic and biotic factors interact at various scales to influence treeline elevations in nonlinear ways that are challenging to predict (Holtmeier & Broll 2005; Resler 2006; Malanson et al. 2007). Holtmeier and Broll (2005) argued that in order to provide a climatic context and better understand treeline dynamics, the complex interactions between abiotic and biotic processes at treeline must be explained.

To address this challenge, biogeographers and ecologists have regularly applied various statistical approaches that examine the relationships between treeline and multiple abiotic and/or biotic factors. Traditional stepwise logistic regression has often been used outright with minimal alteration of the data (e.g., Driese et al. 1997; Dirnböck et al. 2003; Bader & Ruijten 2008). Logistic regression is popular because nominal (e.g., trees versus no trees) or ordinal (e.g., trees, meadows, bare rock) classifications of vegetation are regularly employed in treeline environments and examined in relation to continuous geophysical data derived from digital elevation models (Brown 1994b). Factor analysis (e.g., Brown 1994b) and/or principal components analysis have occasionally been used in concert with logistic regression to group independent variables into correlated sets that are independent of each other (e.g., Brown 1994b; Hessl & Baker 1997). Stepwise multiple regression is also used (e.g., Walsh et al. 1994), but much less frequently than logistic regression because it requires the treeline classification to comprise continuous data. The top 50 hits of a Google Scholar search using the terms 'alpine treeline' and 'regression' indicate logistic regression is preferred by an 8 to 2 margin over both multiple regression and principal components and/or factor analysis. Other more complex modeling approaches have also been used (e.g., Cairns 2001) to a lesser extent, but we focus on logistic regression in this paper.

In some instances, biogeographers and ecologists may seek to develop the single best explanatory logistic regression model while at other times they try to determine the relative importance of independent variables (e.g., elevation, slope angle and aspect, disturbances, microsite characteristics, and proximity to previously existing trees) in influencing the spatial distribution of trees. However, explanatory independent variables tend to be highly correlated in many treeline studies (Brown 1994b; Stueve et al. 2009) and have the potential to produce spurious results deriving from multicollinearity (Chevan & Sutherland 1991; Mac Nally 1996).

For example, independent variables that are found to be statistically significant may not influence the spatial distribution of a species/functional group or may merely exert a minor statistically insignificant influence, but be erroneously ranked or included in the ‘best’ model because they are correlated with one or more causal variables (Mac Nally 1996; Stueve et al. 2009). Factor analysis and principal components analysis mitigate the effects of multicollinearity and are useful in developing logistic models (Brown 1994b). However, teasing out the differences between the independent variables and indentifying the most important predictors using either approach can be problematic (Bader & Ruijten 2008). In this vein, traditional stepwise logistic regression approaches have been used independently to rank the importance of predictor variables, but the order of the rankings is susceptible to the influences of multicollinearity and this may produce spurious results (Brown 1994b; Mac Nally 1996; Stueve et al. 2009).

Susceptibility to multicollinearity is especially relevant at treeline because both abiotic and biotic independent variables tend to be highly correlated. Under these conditions, Pearson correlation coefficients often approach or exceed the set threshold (i.e., 0.7) used when considering the reliability of inferences gained from traditional logistic regression techniques (Brown 1994b; Stueve et al. 2009). This problem is particularly evident when considering influences on spatial patterns of tree establishment from parameters such as the distance to existing trees and ground elevation. In many cases, tree establishment occurs near existing trees at relatively low elevations. Variables built around these influences (i.e., proximity to previously existing trees, and elevation) are often strongly correlated and exert similar directional influences on tree establishment. This makes it difficult to determine if it is the low elevation and/or the proximity to a previously existing tree that has the greater influence on tree establishment. If we can unambiguously explain relationships like this our understanding of tree establishment will be improved, and biogeographers and ecologists will be in a better position to test the validity of the traditional assumption that treelines are in equilibrium with their physical environment: a crucial assumption when developing and applying static predictive models (Brown 1994b; Miller & Franklin 2002).

Identifying important predictors of tree establishment at treeline is of paramount importance in enhancing our understanding of treeline dynamics, and to achieve this a better understanding of the regression approaches that are used is required. Consequently, the aim of this research is to demonstrate the utility of logistic regression within a hierarchical partitioning framework as a useful tool for ranking the importance of independent variables and improving interpretations of tree establishment at treeline (i.e., versus traditional regression). To do this, we used traditional stepwise logistic regression and logistic regression within a hierarchical partitioning framework to produce sets of statistical rankings of spatially-referenced abiotic and biotic independent variables correlated with mapped locations of trees that established after a fire in a treeline area in Mount Rainier National Park.

4.2 Methods

4.2.1 Study site

Mount Rainier National Park is located about 100 km southeast of Seattle, WA on the western slope of the Cascade Range. Established on March 2, 1899, it is the fifth oldest national park in the U.S.A. and has been written about extensively (e.g., Hemstrom & Franklin 1982; Rochefort & Peterson 1996; Stueve et al. 2009). Within the park, treeline approximately varies from 1500 -2200 m a.s.l. This study is located at a treeline site which was burnt by a wildfire in 1930 on the western slope of Mount Rainier, where altitude ranges from approximately 800-2000 m a.s.l. The trees we have mapped in the study became established after the fire and occur between the 1930 forest line (i.e., highest elevation of closed canopy subalpine forest) and the upper tree limit of 2003 (i.e., highest elevation attained by trees, including krummholz). Downed boles observed in the field and on the 2003 aerial photography helped confirm these boundaries. Further information about the site is available in Stueve et al. (2009).

4.2.2 Data acquisition and processing

Panchromatic KH-4B CORONA photography (~1.9 m spatial resolution) from Mission 1110 in 1970 and a 2003 USGS DOQQ (1.0 m spatial resolution) were used to derive the variables used in this analysis. The processing of these data is described in Stueve et al. (2009). A binary classification of pixels with and without trees was generated for each image. Pixels that were treeless between 1970 and 2003, and pixels in which trees had established themselves after 1970 and still persisted in 2003 were identified. We digitally clipped these pixels from those that contained trees in 1970 and 2003, and those that contained trees in 1970 but became treeless in 2003 (< 0.5% of all pixels). The clipped pixels served as the dependent variable in the regression analyses.

Independent variables thought to be important in controlling treeline were derived from a LIDAR-based DEM at a spatial resolution of 1.8 m (Terrapoint 2003), ancillary climate data, pixels identified as having trees in 1970 relative to those pixels in which trees became established after 1970, and a spatially-weighted matrix representing spatial autocorrelation (Stueve et al. 2009). The DEM is a bare-ground model (tree tops removed) that was processed before elevation values were extracted along with derivations of slope aspect and angle that considered all eight surrounding pixels in a 3x3 window. Potential depth of winter snowpack was derived from southwesterly prevailing winds and topographic variability modeled with the DEM (e.g., windward and convex slopes are weighted with lower potential snowpack compared to leeward and concave slopes). The descriptor ’potential’ is used for this, and other parameters, because it is not a direct measure of snow depth. Rather, it represents the relative differences in snow depth across the landscape given the amount of snow that would have fallen in a year. The ranges of values for all ‘potential’ indices were scaled to between -2.5 and 2.5 with negative values representing lower potential and positive values higher potential. Topographic variability modeled with the DEM was also used to derive the wetness potential (e.g., convex slopes with a limited upslope catchment area are weighted with a lower wetness potential compared to concave depressions with large upslope catchment areas) and erosion potential (e.g., ravines and streams with large upslope catchment areas are the most prone to erosion). Euclidean distance was used to measure proximity to 1970 trees. The centroids of pixels that were classified as ‘trees’ in 1970 served as the starting point for distance calculations. Only those pixels that were treeless in 1970 and adjacent to pixels classified as ‘trees’ served as starting points (Figure 4-1).

Direction from 1970 trees was derived from the same pixels as proximity to existing trees (i.e., pixels classified as ‘treeless’ in 1970 were identified as being on the N, NE, E, SE, S, SW, W, or NW side of trees that existed in 1970) (Figure 4-1). Spatial autocorrelation was modeled as the final independent variable using the Delaunay triangulation, which was selected via data-driven Akaike information criterion rankings (Dray et al. 2006). Before performing the regressions, we used a stratified random sampling scheme to extract 1000 points from the data in order to collect a representative sample from the wide range of independent variables to ensure statistical rigor.
Spatial preferences for post-1970 tree establishment have been reported by Stueve et al. (2009): these are close proximity (< 50 m) to 1970 trees, at elevations between 1250-1350 m, on moderate (40-60°) slopes, in sheltered (W, NW, N, NE, and E) aspects, in relatively xeric conditions, on protected sides of 1970 trees (NW, N, NE), and at sites with intermediate snowpack.

4.2.3 Statistical Analyses

We applied four different statistical tests to the data. The Pearson correlation test was used to examine the independent variables for multicollinearity. Backward and forward stepwise logistic regression (two traditional approaches) and logistic regression

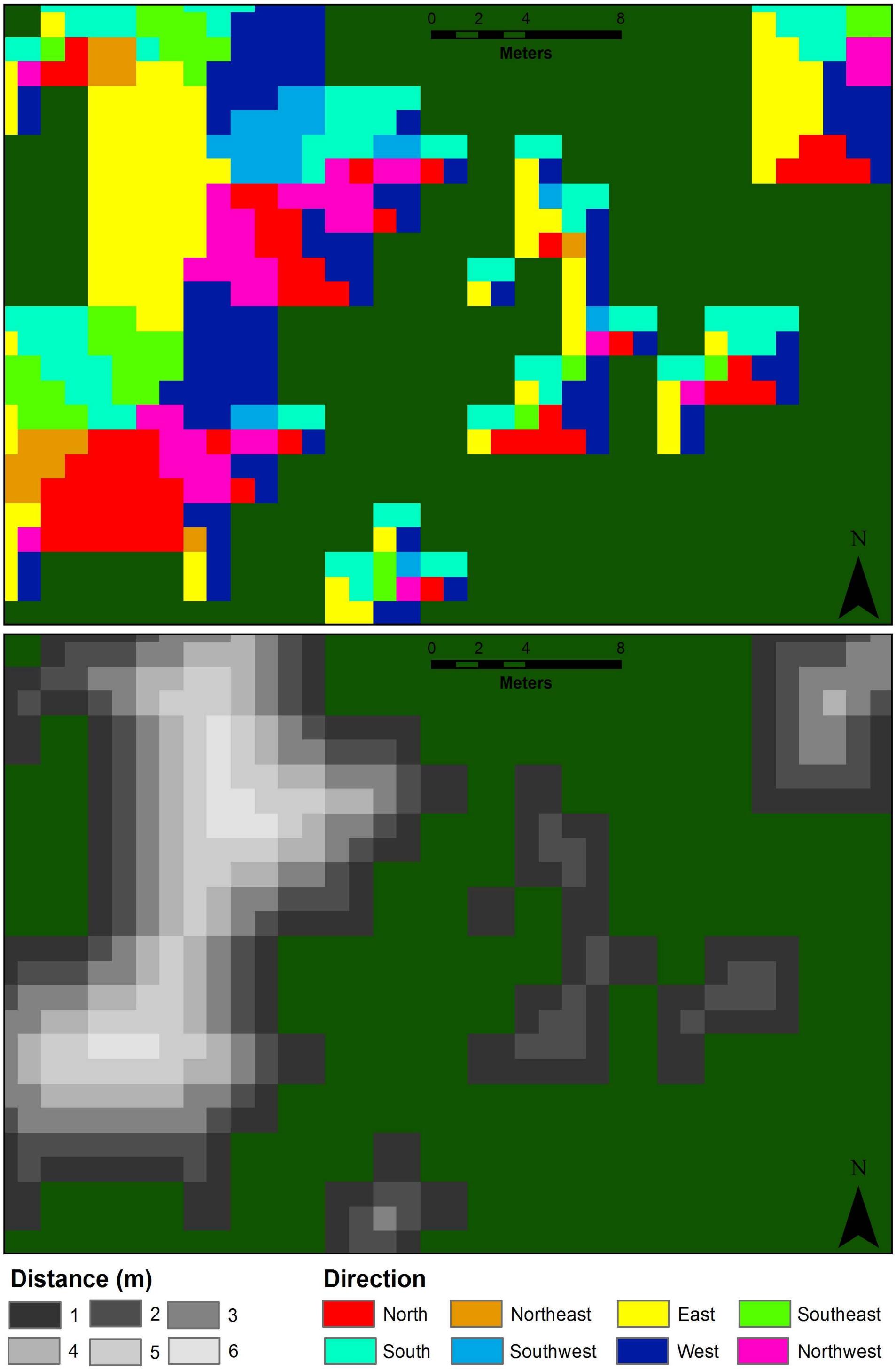


Figure 4-1: Raster delineations representing 'proximity to 1970 trees' (bottom) and 'direction from 1970 trees' (top). 1970 trees are denoted by dark green.

within the hierarchical partitioning framework (the alternative approach) were used to rank the importance of the independent variables.

4.2.4 Pearson's test

Pearson's correlation test is a classic measure of linear correlation between variables that is widely used in biogeography (e.g., Berendse et al. 2001):

$$r = \frac{\sum_{i-1}^{n}\left(X_i - \overline{X}\right)\left(Y_i - \overline{Y}\right)}{\left(n-1\right)S_X S_Y}$$

where X and Y are independent variables with corresponding means $\left(\overline{X}, \overline{Y}\right)$ and standard deviations (S_X, S_Y). This test is commonly applied before performing logistic regression to determine if there is multicollinearity among the independent variables that may compromise results. It is inappropriate to use traditional stepwise logistic regression if specific Pearson's correlation thresholds are exceeded. Hosmer and Lemeshow (2000) recommend that no two independent variables exceed the 0.7 threshold, but others (e.g., Hessl & Baker 1997) consider 0.5 to be overly correlated.

4.2.5 Traditional binomial logistic regression

We used SPSS v.12.0.1 for Windows (2004) to perform traditional binomial stepwise logistic regression and test the null hypothesis that tree establishment patterns were not related to local site conditions. We selected this approach because it is widely used, the dependent variable is dichotomous, and it has less stringent assumptions in terms of normally distributed variables, homoscedasticity, and linearity between the dependent and independent variables (Hosmer & Lemeshow 2000). Both backward (variables removed one at a time) and forward (variables added one at a time) logistic regression were used to analyze the data and determine what independent variables were most important in controlling tree establishment patterns. We chose to implement both because they have been known to provide contradictory rankings and having consistent results between both approaches lends more credence to the rankings (Kupfer et al. 2008). The following equation describes the basic logistic regression approach:

$$Y = \ln [p / (1-p)] = ß_0 + (ß_1 X_2) + (ß_2 X_2) + (ß_3 X_3) \ldots (ß_n X_n)$$

where ln is the natural logarithm, p is the probability of obtaining a positive response, $ß_{0,}$ $ß_{1,}$ $ß_{2, \ldots}ß_n$ are parameters estimated from observed data, and X_1, X_2, X_3,…, X_n are independent variables. The potential inclusion of variables at each step was determined using the stepwise likelihood ratio method with a level of $P = 0.05$ for entry and $P = 0.10$ for removal.

Scatterplots were assessed to determine whether independent variables were linearly related to the logit of the dependent variable. The square root, quadratic, and logarithmic transformations were used to diminish the effects of nonlinearity and also to lower skewness and kurtosis values near 0.5. We used the Wald statistic to rank the importance of independent variables and calculated confidence interval thresholds to determine whether rankings were statistically different (Agresti 1996). The Wald statistic tests the significance of the model coefficient and is calculated by dividing the model coefficient by the corresponding standard error and squaring the result. The Wald statistic is superior to the beta coefficient in identifying important independent variables because it is not as susceptible to extreme values in the independent or dependent data (Cumming 2000). The most important independent variables correspond with larger Wald values.

4.2.6 Binomial logistic regression within the hierarchical partitioning framework

Chevan and Sutherland (1991) discussed a logistic regression method based on the mathematical hierarchical theorem. Later, Mac Nally (1996, 2000, 2002) promoted the potential contributions of such an approach in ecological research and introduced it in the statistical package *R*. Hierarchical partitioning calculates incremental improvements of traditional regression models by incorporating a given variable and averaging its effects throughout all possible combinations with other variables (Mac Nally 1996). For example, consider the effects of some independent variable (*A*) on all first-order, second-order, third-order, and higher-order models (as discussed by Mac Nally 1996). If *A* has a significant independent influence, model fits for any of the first- and higher-order models will be better when *A* is included. In hierarchical partitioning, all possible combinations of variables in regression models are thoroughly and consistently assessed in this manner. Such an approach has been posited to mitigate the effects of multicollinearity and provide a more reliable ranking of independent variables (Mac Nally 1996).

We executed this approach on the transformed data (i.e., from the traditional logistic regression section) using *R 2.4.1* (2006) to test the null hypothesis that tree establishment patterns were not related to local site conditions. The randomization method was also employed to calculate Z-values, define upper and lower thresholds of confidence, and gauge whether or not each of the respective independent variables were statistically significant (Mac Nally 2002).

4.3 Results

The Pearson's correlation test indicated that none of the independent variables exceeded the 0.7 threshold recommended by Hosmer and Lemeshow (2000) (Table 4-1). Two pairs of variables closely approached this threshold (proximity to 1970 trees and elevation, and wetness and erosion potentials) (Table 4-1). Consequently, these two pairs exceeded the more cautious interpretation of correlation coefficients where 0.5 is the threshold, signifying that multicollinearity may be problematic with traditional logistic regression. Slope angle was also moderately high (near 0.5) when considered as a pair with elevation and proximity to 1970 trees (Table 4-1). As a precaution, we performed two series of regressions. One included all independent variables; the second excluded all independent variables with correlation coefficients near and beyond the threshold of 0.5 (i.e., excluding proximity to 1970 trees, elevation, and wetness potential).

In terms of the logistic regressions, we were able to reject the general null

Table 4-1: Pearson correlation coefficients (top line of each pair) and corresponding significance values (bottom line of each pair) between the independent variables used in the regression analyses. For some ecologists, a threshold beyond 0.7 is indicative of overly correlated variables. Others contend that those beyond 0.5 are strongly correlated, and my introduce errors with the implementation of traditional regressions.

	Elevation	**Proximity to 1970 Trees**	**Direction from 1970 Trees**	**Slope Aspect**	**Slope Angle**	**Snow Potential**	**Erosion Potential**	**Wetness Potential**
Elevation	1	------	------	------	------	------	------	------
	0.000	------	------	------	------	------	------	------
Proximity to 1970 Trees	0.696	1	------	------	------	------	------	------
	0.000	0.000	------	------	------	------	------	------
Direction from 1970 Trees	0.207	0.261	1	------	------	------	------	------
	0.000	0.000	0.000	------	------	------	------	------
Slope Aspect	0.224	0.280	0.358	1	------	------	------	------
	0.000	0.000	0.000	0.000	------	------	------	------
Slope Angle	-0.408	-0.468	0.019	0.122	1	------	------	------
	0.000	0.000	0.275	0.000	0.000	------	------	------
Snow Potential	-0.216	-0.196	0.129	0.017	0.194	1	------	------
	0.000	0.000	0.000	0.295	0.000	0.000	------	------
Erosion Potential	-0.139	-0.098	0.344	0.248	0.318	0.424	1	------
	0.000	0.001	0.000	0.000	0.000	0.000	0.000	------
Wetness Potential	0.107	0.219	0.287	0.173	-0.204	0.289	0.666	1
	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

hypothesis in all cases and accept the alternative hypothesis that local site conditions were related to tree establishment patterns (i.e., they were not random). However, there were some discrepancies in the results.

4.3.1 Regressions including all independent variables

The Wald Statistic indicated that slope angle (~60) was clearly the most important independent variable when using either backward or forward logistic regression (Figure 4-2). Proximity to 1970 trees, erosion and wetness potentials, elevation, and slope aspect were also important contributors. Direction from 1970 trees and snow potential were not significant at < 0.01, and they were excluded from the relative rankings.

Conversely, logistic regression within the hierarchical partitioning framework yielded results that were quite different than those from traditional regression. With this approach, we found the most important independently ranked predictor of tree establishment patterns was proximity to existing trees (~15%) (Figure 4-2). Elevation ranked a close second. Slope angle, slope aspect, wetness potential, direction from 1970 trees, and snow potential were also significant independent variables. We excluded erosion potential from the relative rankings because it was not significant at < 0.01.

4.3.2 Regressions excluding correlated (at > 0.5 threshold) independent variables

When excluding pairs of variables with coefficients near or > 0.5, the ranked order of importance for both backward and forward logistic regression was slope angle, slope aspect, and direction from 1970 trees (Table 4-2). The first three ranked variables from the alternative hierarchical regression approach were consistent with the traditional regression approaches. The only difference with this regression approach was the inclusion of snow potential as an additional statistically significant variable (Table 4-2). Snow potential barely exceeded the < 0.01 threshold of statistical significance when applying the hierarchical regression approach, but was just below the threshold with the traditional regression approaches. Associated Wald statistics and the percent independent contributions were relatively low (i.e., < 27.5 and < 3.3 respectively) when compared to those that included all variables. The ranked order of variables in both the traditional and hierarchical regression approaches also corresponded with the relative rankings in the hierarchical regression approach that considered all of the independent variables (in descending order of importance these are slope angle, slope aspect, direction from 1970 trees, and snow potential are highlighted as important predictors) (Table 4-2 and Figure 4-2).

4.4 Discussion

A standard measure of confidence in the results of the application of a particular regression technique is how well it corresponds to other regression approaches applied to the same data set (e.g., Kupfer et al. 2008). If the order of importance of the variables, and the relative changes between the variables (e.g., linear versus exponential decrease in importance), differs between techniques; a researcher’s confidence in ranking the importance of independent variables is low, and questions arise about the interpretations of the data in the context of the research.

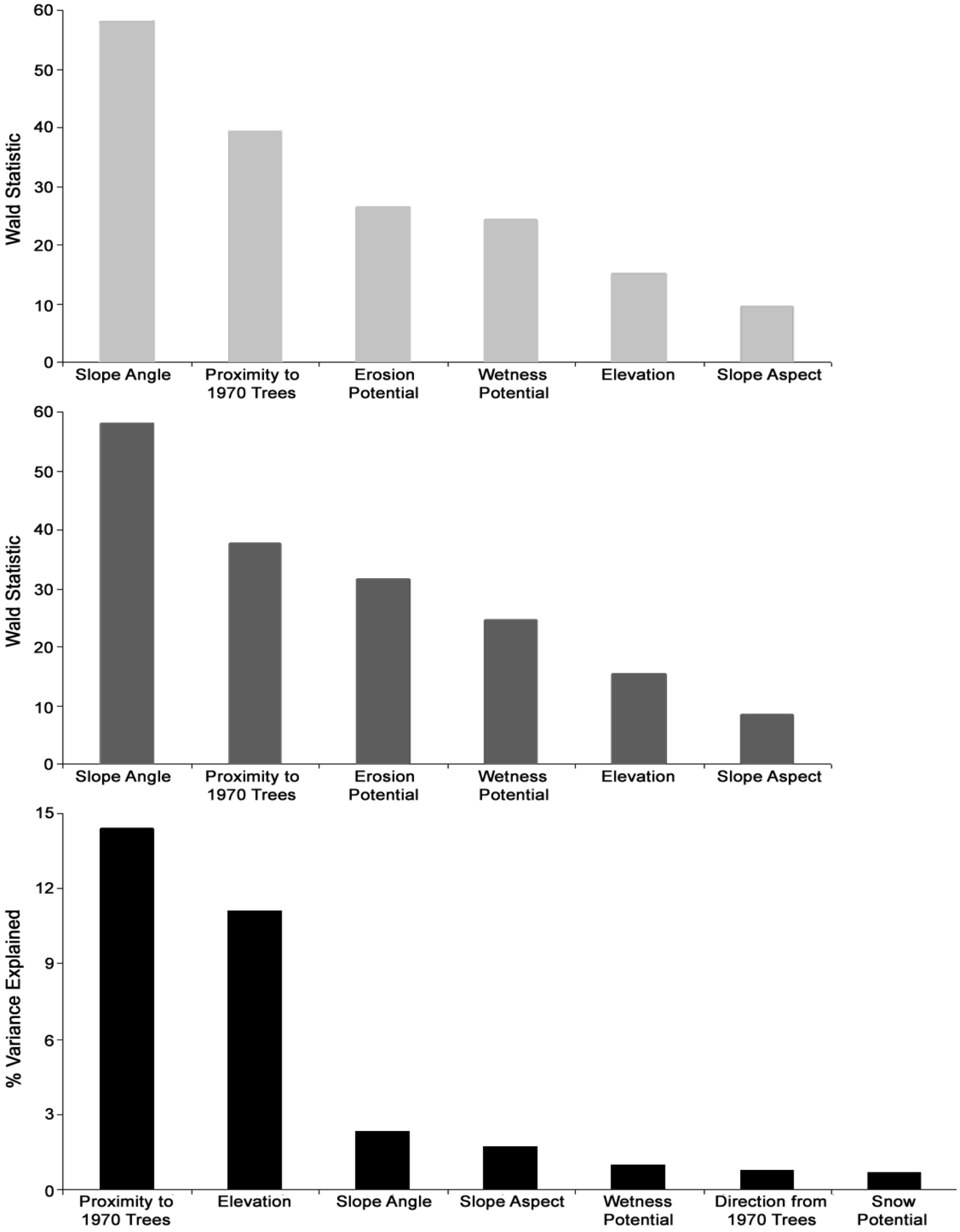


Figure 4-2: Rankings of independent variables from backward stepwise (top), forward stepwise (middle), and hierarchical partitioning (bottom) logistic regressions. All variables were included in the regression analyses, but variables that were not significant at < 0.01 were excluded from the rankings. Upper and lower confidence intervals overlapped for erosion potential and wetness potential (top); wetness potential, direction from 1970 trees, and snow potential (bottom); slope angle and slope aspect (bottom); thus indicating no statistical difference between these respective rankings.

Table 4-2: Ranked order of importance for all three regression approaches when considering only independent variables with Pearson correlation coefficients < 0.5. Variables not significant at < 0.01 were excluded from the rankings. [1] represents the Wald statistic and [2] the independent percent variance explained. Upper and lower confidence intervals overlapped for direction from 1970 trees and snow potential (Hierarchical), indicating no statistical difference for these rankings.

Type of Logistic Regression	**Ranks of Independent Variables with Pearson Coefficients < 0.5**	**Wald Statistic[1] and % Variance Explained[2]**
Backward	(1st) Slope Angle	27.5^1
	(2nd) Slope Aspect	18.9^1
	(3rd) Direction from 1970 Trees	11.7^1
Forward	(1st) Slope Angle	27.7^1
	(2nd) Slope Aspect	16.8^1
	(3rd) Direction from 1970 Trees	14.6^1
Hierarchical Partitioning	(1st) Slope Angle	3.3^2
	(2nd) Slope Aspect	2.2^2
	(3rd) Direction from 1970 Trees	0.8^2
	(4th) Snow Potential	0.6^2

Our analyses indicated that even moderately high correlations (e.g., near and > 0.5) between independent variables introduced uncertainty in relative rankings when employing logistic regression to all variables. Discrepancies in the ranked order of independent variables between the traditional and hierarchical regression approaches is the first indicator that multicollinearity between the independent variables may be introducing uncertainty in the analyses. However, it is difficult to conclude which regression approach is producing the ‘correct’ result by simply comparing the rankings.

When examining the results presented above more closely, the approximately linear decrease from the most importantly ranked independent variable to the least important introduces some skepticism about the traditional regression approaches (Figure 4-2). This trend indicates that one or more of the most important independent variables may be distributing their explanatory influence with other variables that they are correlated with in the sequence, thereby increasing the significance of the lower ranked variables (e.g., Lagos et al. 2008). Conversely, the ranked order of independent variables evident with the hierarchical regression approach exhibited an exponential decrease in importance. This suggests that the explanatory influences of overly correlated variables are not being allocated amongst other variables and that proximity to 1970 trees and elevation are clearly the two most important independent variables.

Additional doubt is cast on the traditional regression approaches when only poorly correlated independent variables (i.e., with Pearson correlation coefficients < 0.5) are used in the regression analyses; providing further evidence that multicollinearity is introducing spurious results with this approach. Consistency between the rankings of all three regression approaches (Table 4-2) provides a high level of confidence in the order of these rankings (Table 4-2). However, some crucial differences are evident when comparing these results to the regression analyses that included all independent variables.

Despite the inclusion of three highly correlated independent variables (i.e., proximity to 1970 trees, elevation, and wetness potential) in the hierarchical regression approach that considered all independent variables, the relative importance of the variables matched the ranked order of the three different regression approaches that included the poorly correlated variables. For the poorly correlated variables, slope angle, slope aspect, and direction from 1970 trees were statistically significant. The relative importance of these independent variables remained the same in the hierarchical regression approach that included all independent variables. Conversely, only slope angle and aspect were statistically significant when we applied the traditional regression approaches to all independent variables. More importantly, values for the Wald statistic are comparatively low and values for the percent independent contributions are similar when comparing the results of poorly correlated variables with all variables (Table 4-2). For example, the Wald statistic for slope angle is near 27 (poorly correlated variables) but it increases to nearly 60 when using all variables. Alternatively, the percent independent contribution for slope angle with the hierarchical regression approach is just above 3 (poorly correlated variables), which is only slightly higher than the result when using all variables. This trend strongly suggests that the ranked importance of slope angle and other independent variables are being influenced by multicollinearity between the independent variables.

One additional piece of evidence reduced our confidence in the results of the traditional regression analyses that used all independent variables. Elevation is widely assumed to exert a significant influence on treeline dynamics at both disturbed and relatively undisturbed treelines (e.g., Shankman 1984; Körner 1998; Stueve et al. 2009). However, it was only marginally significant when traditional regression approaches were used. This again suggests that multicollinearity between the independent variables may be introducing uncertainty in the rankings.

We remain skeptical about the results provided by the traditional logistic regression analyses when all of the independent variables were used. An expanding body of literature continues to caution against using the traditional regression approach for many reasons (James & McCulloch 1990; Whittingham et al. 2006), but particularly when even moderate degrees of multicollinearity exist amongst the independent variables (Mac Nally 2000). This is the case with this dataset. Some biogeographers and ecologists even question the validity of previously published research that employs such techniques (e.g., Whittingham et al. 2006). Unlike traditional logistic regression, hierarchical partitioning allows all combinations of independent variables to be considered and reduces the level of uncertainty in their relative rankings. This approach may lend more credence to future treeline studies and enhance the theoretical development of treeline ecology.

4.5 Conclusions

Biogeographers and ecologists examining treeline dynamics typically utilize the relative rankings of statistical analyses to develop the structure and corresponding theoretical discussions in their research papers. The most important predictors are regularly used to lend support to hypotheses and, ultimately, develop theory. However, statistical approaches are constantly changing, prone to misuse, and susceptible to the introduction of questionable levels of uncertainty (James & McCulloch 1990; Stephens et al. 2007). Our comparative analysis unequivocally demonstrates the potential for uncertainty and decreased confidence in the rankings provided by traditional regressions.

Selecting the correct regression approach for biogeographic and ecological research is crucial because the resulting analysis has the potential to sway research discussions and, ultimately, the theoretical advances emanating from research. If this had been a relatively undisturbed treeline, the results from the hierarchical regression approach may have stimulated a discussion challenging assumptions of equilibrium in treeline environments because of the dominant influence of the proximity to existing trees on establishment patterns of new trees. Conversely, the traditional regression approaches would have reinforced commonly held assumptions. Multicollinearity between independent variables is and will continue to be a serious concern in treeline studies. We assert that logistic regression within the hierarchical partitioning framework should at the very least complement, if not supplant, traditional logistic regression in future tree establishment studies in similar environments. If traditional logistical regression is used, biogeographers and ecologists must ensure that only weakly correlated independent variables are included if their results are to be meaningful.

CHAPTER V

POST-FIRE TREE ESTABLISHMENT PATTERNS AT THE ALPINE TREELINE ECOTONE: MOUNT RAINIER NATIONAL PARK, WASHINGTON, USA*

5.1 Introduction

The alpine treeline ecotone (treeline) exhibits one of the most striking transitional physiognomic landscapes, which has garnered attention from vegetation scientists interested in assessing the floristic impacts of climate change (Walther 2003). Treelines often display remarkable variability in structure and composition between different regions, thus contributing to a wide range of definitions (Holtmeier 2003). Simply stated, the treeline demarcates the boundary between closed forests at low elevations and the alpine tundra at high elevations. In the Pacific Northwest, this boundary is characterized by a broad ecotone extending from closed canopy forest through subalpine parklands, to the scrub line or upper limit of trees (Franklin & Dyrness 1988). The subalpine parkland

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* Reprinted with permission from “Post-fire tree establishment patterns at the alpine treeline ecotone: Mount Rainier National Park, Washington, USA” by Kirk M. Stueve, Dawna L. Cerney, Regina M. Rochefort, and Laurie L. Kurth, 2009. *Journal of Vegetation Science*, vol. 20, pp. 107-120, Copyright 2009 by International Association for Vegetation Science, John Wiley & Sons, Inc. (Appendix A).

is comprised of a mosaic of tree clusters and herbaceous vegetation, often extending over an elevation gradient of 300-400 m. The upper limit of this zone is variable and may be composed of krummholz (German for short crooked trees) or upright arboreal vegetation.

The traditional paradigm contends that temperature controls altitudinal limits of treelines and that observed upslope advance is the most likely response to climatic warming (cf. Daniels & Veblen 2003). However, others caution that disturbances (Daniels & Veblen 2003; Cairns & Moen 2004) and variability of tree responses to local site conditions (Miller & Halpern 1998; Holtmeier & Broll 2005) may confound interpretations, making any direct connections to climate tenuous. Reports of relatively stable treelines over the last 50 years warrant these concerns (e.g., Cuevas 2002; Klasner & Fagre 2002). The paucity of known relationships between disturbance events, climate, local site conditions, and altitudinal limits of treelines necessitates additional research to place observed treeline positions in a climatic context (Daniels & Veblen 2003; Holtmeier & Broll 2005).

Many treeline studies are intentionally executed at relatively undisturbed sites in an attempt to correlate results with climatic fluctuations and thus avoid what is perceived to be confounding influences from disturbances (e.g., Cuevas 2002). We assert that disturbed treelines are equally useful to study, given that upslope advance of treelines is often impeded by local site conditions, despite favorable climatic influences, and that some treelines are relicts of past climates (Holtmeier 2003; Lingua et al. 2008). Local site conditions that structure establishment patterns (i.e., spatial arrangement of newly established trees) at disturbed treelines may resemble those at relatively undisturbed sites. Thus, studying both can contribute to a better understanding of factors controlling treeline.

Fire is an important disturbance agent capable of destroying existing trees and depressing the altitudinal limits of treelines (Wilson & Agnew 1992; Noble 1993). Many studies have utilized field plots and dendroecology at local scales to assess treeline recovery after a fire event. Bollinger (1973), for instance, analyzed tree rings from the Colorado Front Range and concluded that fire suppresses treelines to new climatically controlled positions where recently established herbaceous cover inhibits treeline recovery. In the same study area, Peet (1981) argued that fire and climate cause treelines to exist in dynamic equilibrium, whereby treelines recover slowly after a fire event, with the highest rates of establishment occurring uniformly near existing trees. He predicted future fires would prevent treelines from reaching altitudinal limits controlled by climate. Shankman (1984) demonstrated that the Colorado Front Range treelines slowly established upslope after a fire disturbance, with the greatest recovery rates occurring at low elevations and in close proximity to existing trees. He posited that treelines could recover to their original altitudinal limits gradually and in a uniform manner, provided that there are no additional disturbances.

Additional studies have illustrated the importance of local site conditions. Agee & Smith (1984) determined that close proximity to patches of surviving trees and lack of deep snow cover were directly related to the highest rates of establishment after fire in the Olympic Mountains, Washington. In the Colorado Front Range, Shankman & Daly

(1988) determined that topographically sheltered sites exhibited high rates of establishment after fire and predicted that the treeline would return to its pre-disturbed altitudinal position in a patchy manner. They also noted that a few topographically exposed sites having xerophytic tree species experienced increased rates of establishment. Noble (1993) developed raster-based models depicting interactions between fire disturbance, climate, and subsequent establishment at the treeline. He proposed that up-slope treeline advance after fire would be episodic and exhibit heterogeneous establishment patterns.

Clarifying the importance of local site conditions in structuring establishment patterns at the treeline requires the use of a complex landscape ecological approach (Holtmeier 2003). We used satellite imagery, aerial photography, digital terrain data, and ancillary climate data in a GIS environment to explain landscape-scale patterns of establishment at a treeline disturbed by a 1930 fire in Mount Rainier National Park. We suspect that establishment and upslope advance of the forest line will be evident because climate has been generally favorable (i.e., warm and dry summers) throughout the 20th century, particularly on the western slopes of Mount Rainier (Rochefort & Peterson 1996; Miller & Halpern 1998). Landscape heterogeneity will probably decrease near the forest line because of increased seed availability and less stressful environmental conditions. Whereas, we expect heterogeneity will increase beyond the forest line because of distance-and elevation-induced seed dispersal decay combined with a tendency for opportunistic establishment in an increasingly unfavorable environment. We also expect favorable locales to exist throughout the abiotic setting (e.g., slope aspect, slope angle, moisture potential, snow potential, and erosion potential), and these will be important in structuring establishment patterns with increasing upslope distance from the forest line.

5.2 Methods

5.2.1 Study area

Mount Rainier (4392 m) is a well-known volcano and the sister mountain to Mount Fuji in Japan. The volcano is nearly symmetrical and is located in the Cascade Range in Washington State, USA (Figure 5-1). Deep valleys and many steep ridges consisting of andesite scoured by Pleistocene and early Holocene glaciers dominate the landscape. Along with glacial drift (Crandell 1969), this has created complex topographic features with widely varying microclimates that often influence patterns of treelines (Rochefort & Peterson 1996). Climate in the region can be characterized as humid temperate, with the majority of seasonal precipitation falling as snow or rain during cool winters (Bailey 1995). Prevailing southwesterly winds create a pronounced orographic effect, resulting in heavy annual snowfall of 1000-2000 cm year $^{-1}$ on the western slopes of Mount Rainier (Hemstrom & Franklin 1982; Bailey 1995). Data from the Longmire weather station (elevation 842 m; Figure 5-1) (1978-2006) indicate average monthly temperature ranged from -0.31^{C} in December to 16.01^{C} in August, average annual precipitation (rain and melted snow) was 201.4 cm, and average annual snowfall was 344.2 cm.

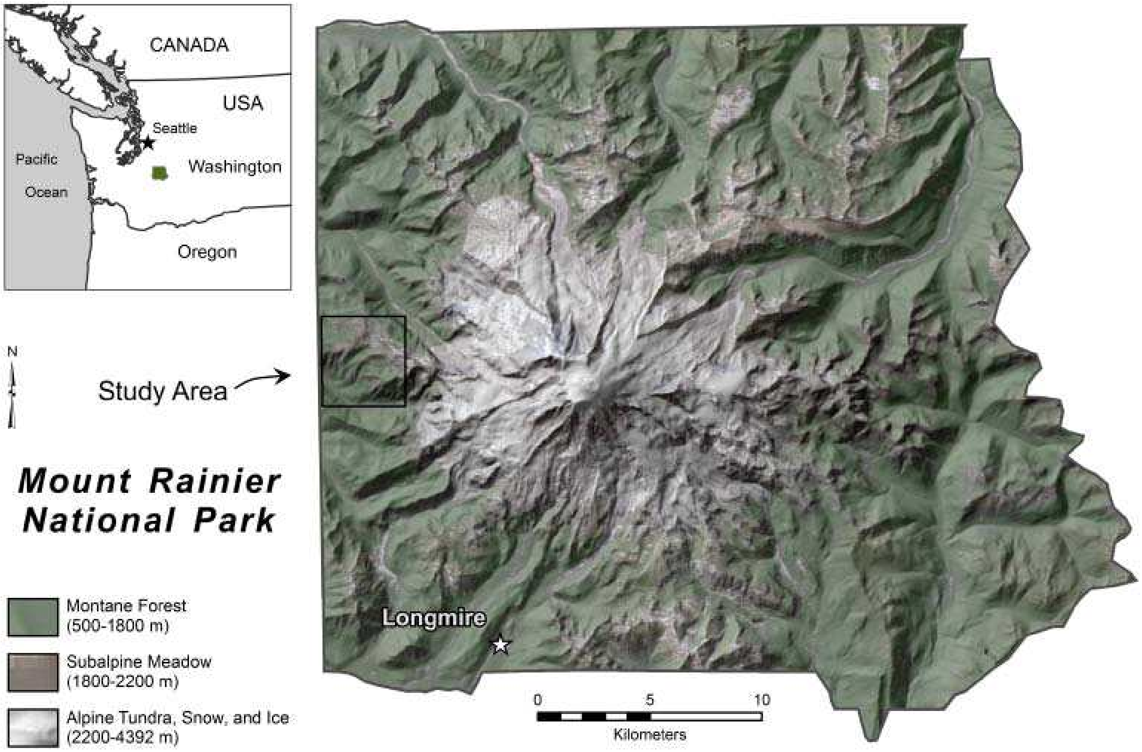

Figure 5-1: The study area as denoted by modified September 2000 Landsat ETM+ imagery and a shaded 10-m DEM.

Snowpack may persist well into August on the western slopes, thus shortening the growing season and contributing to relatively depressed treeline elevations (~1500 m) compared to the eastern slopes (~2200 m) and other western USA treelines (Taylor 1922). The patchy structure of the subalpine parkland is thought to be primarily maintained by the depth and duration of snowpack (Henderson 1974; Franklin & Dyrness 1988). Treeline conifers include *Abies lasiocarpa*, *Chamaecyparis nootkatensis*, and *Tsuga mertensiana* that predominate on the mesic western slopes of Mount Rainier.

Pinus albicaulis and *Picea engelmannii* are most common on the xeric eastern slopes (Rochefort & Peterson 1996). Pulses of increased establishment have been documented throughout the western half of the park during periods of warm dry summers (Franklin et al. 1971; Rochefort & Peterson 1996).

Fire is the predominant disturbance agent in the park, having affected over 90% of existing tree stands, including some treelines (Hemstrom & Franklin 1982). A 1930 fire severely burned extensive areas of high-elevation forest and subalpine parkland (1500-1800 m) near the North Puyallup River, effectively lowering the existing treeline (Hemstrom & Franklin 1982). The aerial extent of the study area is defined by the northeast Mount Wow DOQQ, which was broadly impacted by the 1930 fire. The delineated area contains approximately 150 ha of burned treeline and captures part of the steep southwest-northeast elevation gradient from the North Puyallup River (800 m) to over-arching ridges (2000 m). The relatively xeric south and west slopes of the steepest ridges were severely burned to the krummholz (Hemstrom & Franklin 1982). Field surveillance in 2006 did not reveal any notable signs of other disturbances, such as avalanches, insect infestations, or disease.

The burned area includes numerous spurs that dissect broad south-and west-facing slopes containing complex microtopography, which can influence tree establishment patterns. *Abies lasiocarpa* is the most prevalent species near the forest line and at the upper limits of the krummholz. This species is a common invader after subalpine parkland fires, with a preference for mildly xeric sites that are topographically protected (Shearer 1984; Miller & Halpern 1998). Wind-driven seed dispersal may carry seeds up to 80 m beyond sexually mature trees (2 20 years old) (Noble & Ronco 1978). *Pinus albicaulis, Tsuga mertensiana,* and *Chamaecyparis nootkatensis* are also present, but are much less abundant.

5.2.2 Image preprocessing

The United States Geological Survey provided KH-4B satellite imagery from the CORONA mission 1110 for June 2, 1970. The imagery was from the aft camera and scanned at 7 mm, with a spatial resolution of 1.9 m (McDonald 1995). We orthorectified this imagery using a parametric model and nearest neighbor resampling (Jensen 2005), in concert with direct linear transformation and bundle adjustment to build the exterior orientation (Fiore 2001). A 1.0-m United States Geological Survey color DOQQ from 21.07.2003 was used as the base aerial photography to collect ground control points (Davis & Wang 2003). We selected 42 control points that were evenly distributed throughout the 1970 imagery, with a root mean-square error of 0.495 (Jensen 2005). We used a LIDAR-based 1.8-m DEM (Terrapoint 2003) and KH-4B satellite specifications from declassified documents (McDonald 1995) to model the terrain and satellite position during orthorectification. Pre-processing procedures were employed to remove systematic errors from the DEM (Keqi et al. 2003; Rottensteiner et al. 2005) and the Minnaert correction was used to mitigate radiometric variability from the imagery, which is common in mountainous areas (Itten & Meyer 1993).

We implemented similar methods to georeference aerial photography from 1955, but we could not model the position of the airplane because of insufficient metadata. Also, clouds obscured some key areas of establishment in the photography and some locales also appeared to be pixilated. Thus, the photography was not deemed suitable for detailed mapping procedures or inclusion in the landscape metrics and statistical analyses. However, the photography did allow a qualitative assessment of tree locations before 1970.

5.2.3 Imagery classification, treeline identification, and change detection

We used supervised classifications tailored for high-spatial resolution panchromatic imagery to delineate trees in 1970 and 2003 (Bai et al. 2005). The green band of the DOQQ was separated for the classification analysis because the signal closely corresponds to the KH-4B panchromatic band. The green band of the DOQQ was resampled with the nearest neighbor method to match the 1.9-m spatial resolution of the KH-4B imagery (Jensen 2005). Next, we selected 10 000 training points for each classification category representing trees, shadows (from trees), and treeless areas. We implemented a minimum distance supervised classification with a fitted modal filter to assign shadows to either trees or treeless areas, resulting in a binary classification of trees versus treeless areas.

Upper elevations (1500 m and above) in the KH-4B imagery displayed areas of residual snow-pack near some tree patches. We used 1969 aerial photography that lacked snowpack to verify whether any trees were obscured by snow, and the classification was adjusted accordingly.

The forest line was used to determine the lower boundary of the treeline and as an easily identifiable reference point for assessing treeline changes in terms of distance and elevation (Jobbagy & Jackson 2000). We visually identified and digitized the approximate position of the forest line in the 1955 imagery. Forest line in the classified 1970 satellite imagery and 2003 aerial photography was identified by using a GIS to detect the highest altitudinal limits of pixels classified as trees that were contiguously connected to closed forest. We quantified maximum and minimum forest line changes in a GIS by assessing upslope measurements from each pixel in the 1970 forest line that were perpendicular to slope contours. Treeline was defined as all pixels 30 m below the 1970 forest line and continuing to the highest elevations attained by pixels classified as trees in the 2003 aerial photography for inclusion in the landscape metrics and statistical analyses. Last, change detection was performed to identify areas of establishment at the treeline between 1970 and 2003.

5.2.4 Landscape metrics

The spatial complexity and variability of patch mosaics, otherwise known as landscape heterogeneity, often signify the presence of multiple underlying ecological processes (Li & Reynolds 1994). Studying the spatial arrangement of patches in relation to other abiotic and biotic variables can provide valuable insight to potentially causative ecological mechanisms involved in structuring patch mosaics (Li & Reynolds 1994). To characterize the influence of establishment on landscape heterogeneity, we used a robust landscape metric (new contagion index) and establishment rates in six different zones throughout the treeline (Li & Reynolds 1993). Elevated establishment rates combined with a more fragmented or heterogeneous landscape (i.e., low contagion value) in a particular zone indicate unique combinations of specific local site conditions that may be producing an environment more favorable for establishment.

The first zone created (A) began 30 m down-slope from the 1970 forest line and proceeded 100 m upslope, closely following the curvature of the forest line. The remainder (B, C, D, E, and F) was comprised of five separate 100-m zones proceeding sequentially beyond zone A across the subalpine parkland and towards the alpine tundra. We selected 100-m zones because establishment rates beyond the 1970 forest line were sigmoidal, and each zone spanned a particular section of the sigmoidal curve. A new contagion index was calculated for each zone in the 1970 satellite imagery and 2003 aerial photography. Contagion values from 1970 were subtracted from values in 2003. Negative and positive results indicate increased and decreased landscape heterogeneity, respectively. We also determined establishment rates in each zone by dividing the number of pixels classified as trees in 2003 by the number of pixels classified as treeless in the 1970, then multiplying by 100.

5.2.5 Ground verification and accuracy assessment

We marked 60 ground verification points with a WAAS corrected global positioning system and used them to confirm mapped areas of establishment in the 1970 satellite imagery and 2003 aerial photography. Due to poor satellite reception, we marked 23 additional points with an uncorrected global positioning system in patches of old-growth trees. In the field, we visually identified 49 relatively stable points (i.e., 26 barren patches of rocks that did not exhibit recent signs of disturbance or vegetative growth nearby, and 23 patches of large old-growth trees). To verify the ages of young trees mapped on the imagery (i.e., 33 years or less), 15 tree ring cores and 19 cross sections were collected from widely distributed areas (Jensen 2005) within or in close proximity to mapped patches of establishment. We subjected the tree samples to standard processing before counting tree rings and determining tree ages (Fritts & Swetnam 1989). The resulting classification accuracy was 89.2% for the 1970 points and 91.6% for the 2003 points.

5.2.6 Local site conditions

Data for a suite of variables thought to influence establishment patterns were obtained from the processed DEM and ancillary climate data. Elevation values were extracted directly from the DEM. We calculated slope aspect and slope angle with a3x3 window while considering all eight surrounding pixels (Burrough & McDonnell 1998). We calculated snow index values from curvature (Zevenbergen & Thorne 1987; Moore et al. 1991), southwesterly prevailing winds, elevation, slope aspect, and slope angle (Frank 1988; Burke et al. 1989; Brown 1994b). Topographic concavities and leeward slope aspects at high elevations were weighted with the highest snow potential (i.e., likely to have deep season-shortening snowpack). We calculated wetness index values from the upslope catchment area and drainage patterns quantified in the DEM (Beven & Kirkby 1979; Brown 1994b). Enclosed depressions with large upslope moisture catchment areas were weighted with the highest wetness potential (i.e., likely to have moist and cool soils). We determined sediment erosive index values by considering calculations of slope angle and flow accumulation from the DEM (Moore et al. 1993). Steep convex landscape features and open concavities with large upslope moisture catchment areas (e.g., ravines and stream beds) were weighted with the highest erosion potential (i.e., surfaces likely to be regularly disturbed by erosive forces). Proximity to and direction from trees existing in 1970 was calculated with standard Euclidean distance measures using the 1970 trees as source areas.

5.2.7 Statistical analyses

We devised a statistical approach to test the general null hypothesis that establishment patterns were not related to local site conditions. We selected binomial logistic regression for the statistical analyses because the data consisted of a nominal dependent variable with two classes and independent variables with continuous data. To assess the potential of inflated R^2 values associated with multicollinearity, we conducted Pearson correlation tests between the independent variables of 1000 randomly sampled points (Mac Nally 2000). No pairs were found to be greater than the 0.7 threshold recommended by Hosmer & Lemeshow (2000). However, we found that elevation had values above 0.6 when considered with proximity to 1970 trees and slope angle. To mitigate the effects of multicollinearity, we used R 2.4.1 (Anon. 2006) to conduct binomial logistic regression within the hierarchical partitioning framework (Chevan & Sutherland 1991; Mac Nally 1996) and determined the relative amount of variance each independent variable contributed to establishment patterns (Mac Nally 2002). All circular independent variables (i.e., slope aspect and direction from 1970 trees) were sine-transformed to a linear format ranging from -1 (south) to 1 (north) (Zar 1999). The dependent variable was assigned 0 (treeless) and 1 (trees). Independent variables exhibited significant skewness (1.3–1.9) and kurtosis (1.1–1.7). We excluded outliers and modified the data via logarithmic and square root transformations to reduce skewness and kurtosis values below 0.5. We used a modified randomization approach with R 2.4.1 (2006) to obtain Z-values and determine whether the contribution of each independent variable was statistically significant (Mac Nally 2002). Overall, the variance explained by each independent variable with this regression technique can be substantially lower than results acquired from traditional approaches (e.g., stepwise regression) because joint contributions from correlated independent variables and inflated R^2 values are mitigated (Mac Nally 2000).

Failure to account for spatial autocorrelation can confound statistical analyses of ecological phenomena and may result in the erroneous identification of important independent variables and their relative rankings (Griffith & Peres-Neto 2006). To address spatial autocorrelation, we used R 2.4.1 (2006) to implement a modification of the principal coordinates of neighbour matrices approach based on eigenvectors and distance (Dray et al. 2006). We selected the Delaunay triangulation to generate the spatial weights matrix based on data-driven Akaike information criterion rankings. Results consisted of positive (i.e., similar neighbors clustered in space) and negative (i.e., dissimilar neighbors) eigenvalues in continuous data formats that corresponded well with the traditional Moran's I measure of spatial autocorrelation. We included these data as an additional independent variable in the regression analyses (Griffith & Peres-Neto 2006).

We repeated the method for each zone (A-F) discussed with the landscape metrics to gauge whether the abiotic setting becomes more important in structuring establishment patterns with increased upslope distance from the forest line. Two hundred and fifty points were randomly sampled from each zone and subjected to additional tests. After a preliminary analysis, we combined the two zones closest to the forest line (A and B) and the two zones furthest away from the forest line (E and F) because they gave similar results.

5.3 Results

5.3.1 Forest line changes, landscape heterogeneity, and establishment rates

The 1970 forest line was clearly higher than the approximated elevation of the 1955 forest line, but quantifying establishment rates between these dates was not

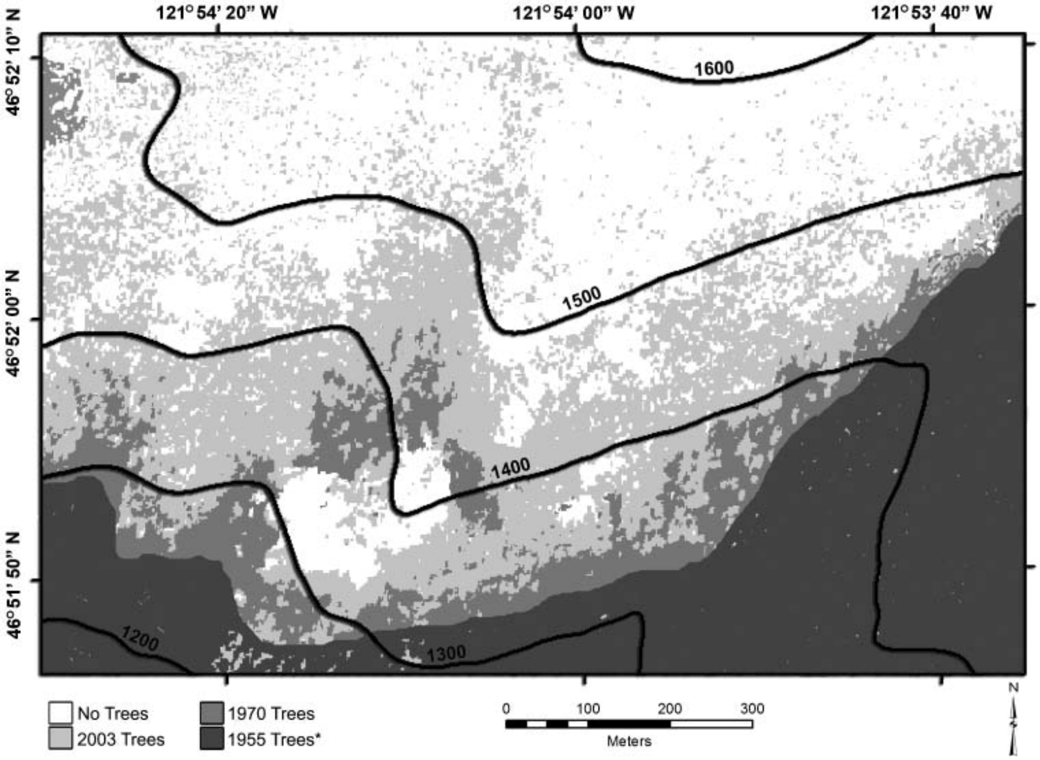

Figure 5-2: Landscape patterns of tree establishment at the study site based off digitized 1955 aerial photography and classification analysis of 1970 CORONA satellite imagery and 2003 aerial photography. Dark gray denotes the approximate location of the forest line and contiguously connected trees in 1955. Medium gray represents trees present in 1970. Light gray represents trees that were newly established after 1970 and prior to 2003. The 1970 forest line follows the northern fringe of continuously connected forest depicted by the medium gray pixels. The 2003 forest line follows the northern fringe of continuously connected forest depicted by the light gray pixels. * indicates an approximation based on observations in a GIS.

possible due to the qualitative methods involved in assessing the 1955 imagery (Figure 5-2). The average elevation of the forest line in the 1970 imagery was approximately 1343 m, with a minimum of 1280 m and a maximum of 1475 m (Figure 5-2). The forest line had ascended upslope by 2003 to an average elevation of approximately 1453 m, with a minimum of 1400 m and a maximum of 1527 m. The smallest altitudinal forest line change between 1970 and 2003 was 0.0 m and the largest was 152 m. The smallest distance of forest line change was also 0.0 m and the largest was 264 m. We observed the majority of establishment near the lowest forest line elevation of 1280 m in the 1970 imagery and the least near the uppermost forest line elevation of 1475 m in the 1970 imagery, with the notable exception of a bare patch between 1300 and 1400 m.

We conducted the following analyses in six zones placed throughout the previously defined treeline area. Contagion difference values were 39% for zone A (Figure 5-3); these decreased in zones B (-36%), C (-45%), and D (-63%) before rebounding slightly in zones E (-62%) and F (-42%) (Figure 5-3). The highest establishment rates occurred in zone A (88%) and steadily decreased in zones B (69%), C (49%), D (42%), E (27%). and F (12%) (Figure 5-4).

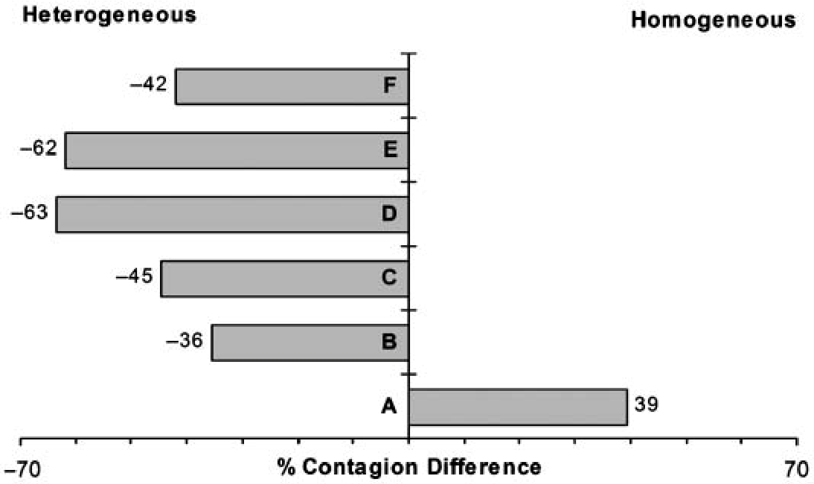

Figure 5-3: Contagion differences measuring landscape heterogeneity changes between 1970 and 2003 for six consecutive 100-m zones. Zone A begins 30 m below the 1970 forest line and zone F is at the altitudinal limit of 2003 trees. Each zone follows the curvature of the forest line.

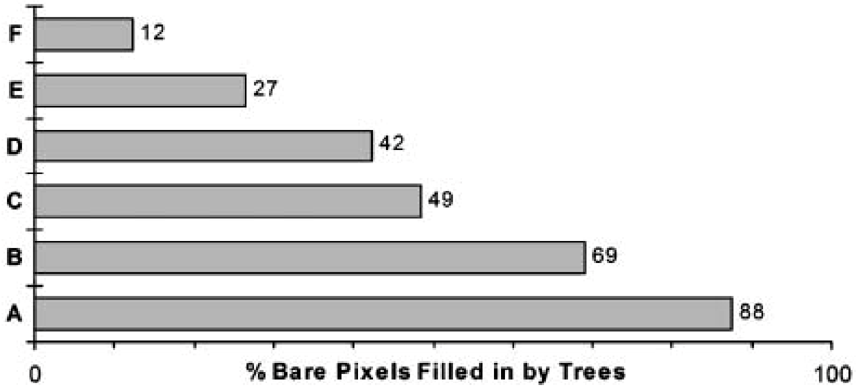

Figure 5-4: Percentage of bare 1970 pixels filled by trees prior to 2003 for six consecutive 100-m zones. Zone A begins 30 m below the 1970 forest line and zone F is at the altitudinal limit of 2003 trees. Each zone follows the curvature of the forest line.

5.3.2 Local site conditions influencing patterns of establishment

We rejected the general null hypothesis and accepted the alternative hypothesis that local site conditions were related to establishment patterns. At a broad spatial scale (i.e., entire study area), we discovered that proximity to 1970 trees (14.1%) and elevation (11.6%) were the two most important local site conditions influencing landscape patterns of establishment (Figure 5-5). Locales within 50 m of 1970 trees experienced the highest rates of establishment (75%), before tapering off at a distance of 300 m (~10%) (Figure 5-6 a). Locales between 1250 and 1350 m experienced the highest rates of establishment (~80%), before gradually decreasing near 1650 m (~0%) (Figure 5-6 b). The elevation response also showed a definitive sigmoidal wave pattern.

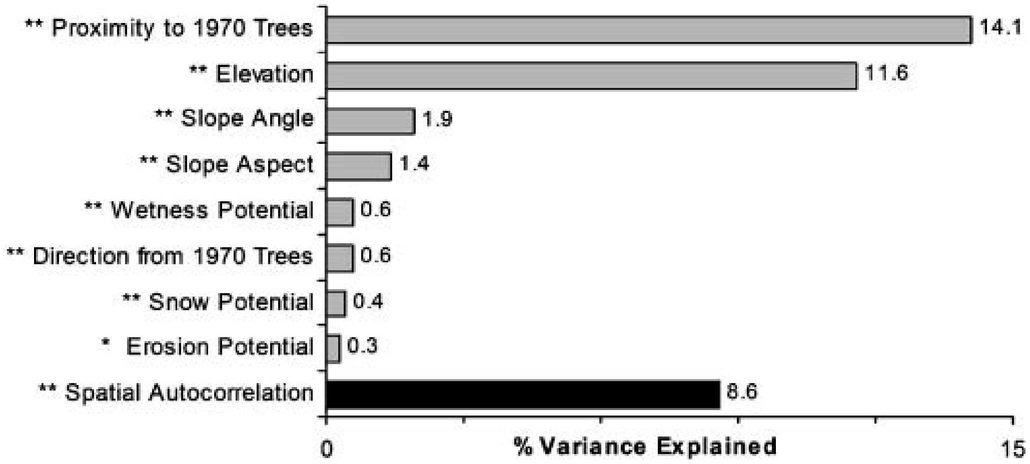

Figure 5-5: Percentage of post-1970 tree establishment variance explained by local site conditions within a defined treeline area from 30 m below the 1970 forest line to the altitudinal limit of 2003 trees. Results are based on binomial logistic regressions employed in the hierarchical partitioning framework when considering the entire study area. ** indicates the independent variable is significant at the 99% confidence level, and * indicates significance at 95%.

Slope angle (1.9%) and slope aspect (1.4%) were also influential in structuring landscape patterns of tree establishment (Figure 5-5). Moderately steep slope angles between 40 degrees and 60 degrees experienced the highest rates of establishment (~75%). Establishment was less likely on slope angles <40 degrees and >60 degrees (~60%) (Figure 5-6 c). In terms of slope aspect, west-, northwest-, north-, northeast-, and east-facing slopes displayed elevated rates of establishment (~80%). Relatively exposed south-facing slope aspects experienced lower establishment rates (~40%) (Figure 5-6 d).

Direction from 1970 trees (0.6%), wetness index (0.6%), snow index 0.4%), and erosion index (0.3%) were also statistically significant variables that influenced tree establishment patterns (Figure 5-5). Leeward and relatively shaded northwest-, north-, and northeast-facing tree patch edges showed the highest rates of establishment.

Decreased rates of establishment occurred on south-facing tree patch edges. Xeric to slightly mesic locales experienced the highest rates of establishment. However, extremely wet locales experienced lower establishment rates. Locales with moderate snow potential displayed elevated rates of establishment, before tapering off near exposed windblown areas and in protected sites with high snow potential. Locales prone to erosion displayed slightly decreased establishment rates compared to protected locales. Individually, none of these local site conditions explained >2% of the potential variance at a broad spatial scale. However, they became more important, along with slope aspect and slope angle, when examined at restricted spatial scales.

When considering the local site conditions in each of the six zones, we observed elevated establishment rates at locales similar to those reported in the three preceding paragraphs. However, there were palpable differences in the statistically ranked order of local site conditions. The two zones nearest the 1970 forest line (A and B) became nearly fully occupied by new trees and thus exhibited suppressed signals. However, we observed results in zone C nearly matching those of the entire study area, except for a peak in the importance of slope aspect (Figures 5-5 and 5-7). Several abiotic factors emerged as very important predictors of establishment with increased upslope distance from the previous zone. Slope aspect (13.1%) was the most important variable in zone D. Slope angle (5.7%) and other abiotic variables also became more important; however, proximity to 1970 trees (11.3%) and elevation (5.8%) remained important predictors in zone D. In zones E and F, the cumulative explanatory power of the local site conditions decreased slightly, with slope aspect (8.5%) and proximity (6.5%) to 1970 trees being the most important.

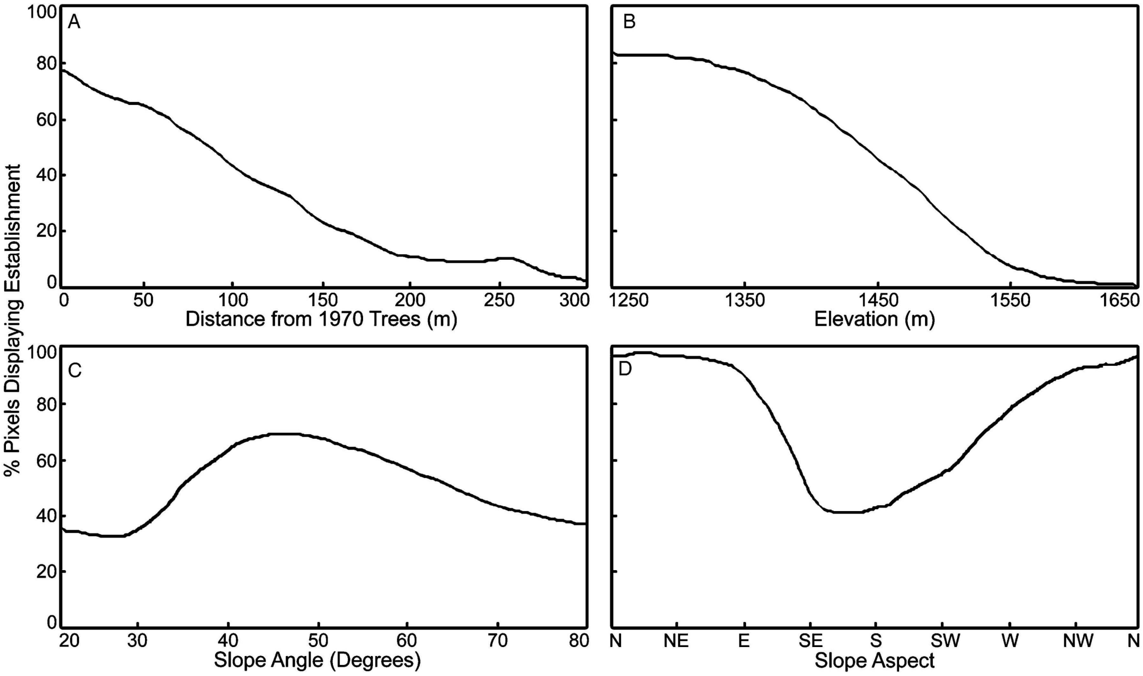

Figure 5-6: Relationships between the four most significant local site conditions and post-1970 tree establishment patterns based on a defined treeline area from 30 m below the 1970 forest line to the altitudinal limit of trees in the 2003 imagery. Values were calculated from 10,000 points used in a stratified sampling scheme in order to reduce spatial autocorrelation. Fractions of pixels experiencing tree establishment were calculated at 50-pixel intervals for each independent variable (i.e., number of pixels classified as trees in the 2003 imagery divided by 50), converted to a percentage, plotted, and connected in a smoothed line graph.

5.4 Discussion

5.4.1 Broad establishment trends

Favorable climatic conditions (i.e., warm and dry summers) probably triggered widespread establishment between 1955 and 2003. Initially, the abiotic setting appeared to play only a minor role in structuring establishment patterns. The majority of establishment occurred near existing trees and at low elevations, regardless of topographic variability; accounting for decreased landscape heterogeneity in zone A and upslope advancement of the forest line. Previous researchers have documented similar establishment patterns after fire disturbance (e.g., Peet 1981; Agee & Smith 1984; Shankman 1984).

We attribute high establishment rates at these locales mostly to increased seed availability from nearby and upslope trees, but also partly to less stressful environmental conditions at low elevations (Agee & Smith 1984; Shankman & Daly 1988; Holtmeier 2003). It is difficult, however, to ignore the possibility that positive feedback mechanisms may be enhancing establishment rates at this site. Contemporary research conducted on positive feedback at the alpine tundra ecotone (e.g., Alftine & Malanson 2004; Bekker 2005; Resler 2006) suggests that it may play a critical role in structuring observed establishment patterns. Mature trees ameliorate the microclimate by increasing soil moisture-holding capacity, moderating soil temperatures, improving nutrient conditions, lengthening the growing season, and protecting seedlings from wind (Little et al. 1994; Weisberg & Baker 1995); thus initiating landscape-scale positive feedback changes into nearby exposed areas (Resler et al. 2005; Cerney 2006; Resler 2006). These assertions are consistent with the literature, which suggests establishment is highest adjacent to clusters of existing trees, before declining with distance in treeline environments (e.g., Peet 1981; Shankman 1984).

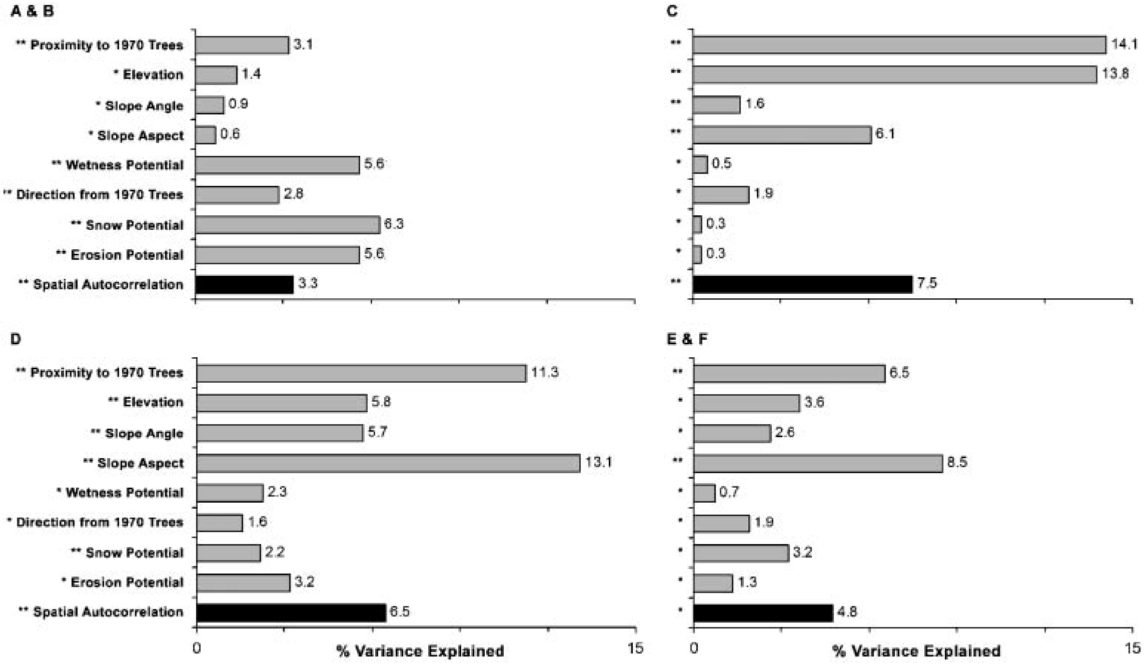

Figure 5-7: Percentage of post-1970 tree establishment variance explained by local site conditions in six zones within a defined treeline area from 30 m below the 1970 forest line to the altitudinal limit of 2003 trees. Distances upslope from the 1970 forest line include 0-200 m (zones A and B), 200-300 m (zone C), 300-400 m (zone D), and 400-600 m (zones E and F). Results are based on binomial logistic regressions employed in the hierarchical partitioning framework. ** indicates the independent variable is significant at the 99% confidence level, and * indicates significance at 95%.

5.4.2 Changing roles of abiotic and biotic factors

Landscape heterogeneity was probably enhanced by reduced tree establishment rates with increases in upslope distance from the forest line (zones B-F). Heterogeneous establishment patterns throughout these zones suggest establishment became more opportunistic and that different local site conditions may be more important at restricted spatial scales. Indeed, the abiotic setting appeared to produce favorable establishment sites (e.g., protected slope aspects, moderate slope angles, moderate snow potential, moderate to low wetness potential, and low erosive potential) at high elevations beyond the forest line (zones C-F) that rivaled or became more important than proximity to existing trees and elevation (Figure 5-7). These heterogeneous establishment patterns match predictions of patchy and variable establishment after fire disturbance, as dictated by a combination of slope aspect, slope angle, soil moisture, and snowpack (Shankman & Daly 1988; Noble 1993).

Potential establishment at high elevations beyond the forest line may be limited by seed dispersal decay, reduced seed viability, and approaching the physiological threshold for trees (Baig & Tranquillini 1976; Tranquillini 1979). Wind Wizard (Butler et al. 2006) suggests that the topography in the study area has a strong effect on winds, forcing the prevailing southwesterly winds, as well as westerly and northerly winds, mostly upslope, which likely carry high quantities of wind-dispersed seed (e.g., *Abies lasiocarpa*) to distant meadows. The upper threshold of seed dispersal decay is probably most limiting to establishment at the highest elevations. However, the abiotic setting appears to be crucial for facilitating establishment within the upslope seed dispersal zone at exposed locales in the harsh environment at high elevations. The sigmoid pattern of establishment we observed with elevation supports this assertion because it indicates competition between patches of different vegetative functional groups and associated influences from ecological site factors are more pronounced at high elevations, thereby reducing establishment rates (Cairns & Waldron 2003).

High rates of establishment on west-, northwest-, north-, northeast-, and east-facing slope aspects can probably be attributed to the existence of narrow diurnal to nocturnal temperature ranges, which produce fewer tree seedling fatalities when compared to relatively exposed south-facing slope aspects that are often subjected to high and low temperature extremes (Germino et al. 2002). Increased rates of establishment evident on moderate slope angles may be higher because soil is more developed than at steep slope angles and is less susceptible to geomorphic disturbances (Holtmeier 2003). Decreased establishment rates observed on shallow slope angles probably occur because existing herbaceous cover is more likely to competitively exclude invading trees (Wardle 1985; Holtmeier 2003). Animal use may also influence vegetation patch dynamics on shallow slope angles (Vale 1987; Veblen et al. 2000). These findings are consistent with the topographic preferences of Abies lasiocarpa.

5.5 Conclusions

This disturbed treeline in this site seems to have entered a phase of rapid establishment, triggered primarily by favorable climatic conditions. If the climate remains favorable, we expect increased seed availability to continue driving widespread establishment near the forest line and near the sexually mature trees. Positive feedback may also be a significant contributor, but our analysis offers mostly circumstantial evidence for this assertion. Reduced rates of opportunistic establishment will likely persist in favorable locales throughout the abiotic setting with increased upslope distance from the forest line. These eco-incursions will probably facilitate the ability of trees to become established and reproduce in the distant tundra; thereby accelerating tree invasions into exposed locales. The concerted effect of these processes will probably cause the treeline to ascend upslope. However, the width of the ecotone may become narrower in the future due to enhanced establishment rates near the forest line. Severely burned areas with few or no surviving trees near the former upper tree limit, on the other hand, may require several additional decades to recover.

It is clear that several abiotic and biotic processes are operating at different spatial scales in this study area. Vegetation scientists have long recognized that plot-scale studies may be susceptible to spatially aggregated processes, but our results indicate this phenomenon may be particularly pronounced at the treeline. Remote sensing, GIS, and spatial statistics should serve a more important role in determining suitable locations of field plots or transects. For example, vegetation scientists could use these tools to identify sites inhibiting establishment in the abiotic setting (e.g., exposed slope aspects with low snow potential) and corresponding plots could be set up to determine if microsite conditions are facilitating limited quantities of establishment in such areas.

Finally, we recognize that parts of the observed establishment patterns remain unexplained. Other variables, such as geologic substrate, edaphic properties, and independent responses of species, could modify the establishment patterns. Remnants of burned boles may also contribute to unique patterns of establishment (Little et al. 1994). These variables were either not available at a spatial grain fine enough for inclusion in this study or were indistinguishable on the photography. Future research may include (1) the use of specialized remote sensing platforms to quantify the electrical conductivity of soils and provide additional detailed edaphic information at the landscape scale, (2) plot-scale studies investigating the influences of microsites (e.g., burned boles) and species-specific responses on establishment patterns, and (3) plot-scale studies directly testing the potential influence from positive feedback. Important questions remain as to how the rankings of local site conditions tested here differ at other treelines. We suspect that the rankings are susceptible to change, particularly under different climate regimes and at other types of treeline.

CHAPTER VI

EVIDENCE OF HIERARCHICAL PATCH DYNAMICS AT AN ALPINE TREELINE DISTURBED BY FIRE?

6.1 Introduction

From the perspective of hierarchy theory, ecosystems are comprised of many asymmetrically interacting systems and subsystems that are interlinked together (Müller 1992). It is crucial to consider the context of the research question(s) being posed when defining ecological hierarchies and how they are to be studied (Schneider 2001). The scale of observation usually plays a critical role in this process along with environmental limitation and biotic potential (c.f. Schneider 2001). The environmental limits of ecosystem processes are defined as the highest hierarchical levels whereas the lowest levels are representative of the biotic potential (c.f. Müller 1997). This hierarchical concept in ecology is old; dating back to 1908 in one case, where it was questioned whether local catches from the Irish Sea could accurately determine the density of organisms in the entire sea (Schneider 2001). Tacit recognition of hierarchy theory persisted throughout the early to middle 20th century (Schneider 2001), but there was little explicit consideration concerning the influence of patch mosaics and spatial heterogeneity until Watt wrote his seminal paper in the *Journal of Ecology* (1947). Watt’s paper was the first directly appreciating the significance of interactions between patch structure and hierarchies of processes in plant communities. He noted in several case studies how assorted processes (abiotic and biotic) may amalgamate with existing patch structures at dissimilar levels or hierarchies in plant communities to influence and dictate plant distribution patterns. He further contended that space and time limited the establishment of species in conjunction with the existing network of patch mosaics. The evidence used to sustain his assertions was limited (at least, in geographic terms) to plant communities in the Breckland Grasslands and Chiltern Hills (in England), and Cairngorm Mountains (in Scotland), but he contended that the conceptual framework of his ideas could be applied beyond these two countries.

After the groundbreaking work of Watt, the frequency of the use of terms such as *hierarchy theory* and *spatial scale* remained low until an exponential growth between the late 1960's and 1990's (Schneider 2001). During the1970's and later, graphical expressions of space-time diagrams exploded, hierarchical concepts were embraced, and landscape ecology rapidly evolved as a new paradigm that incorporated hierarchy theory, spatial heterogeneity, the patch-corridor-matrix, and scale (Forman & Gordon 1981; Forman 1995; Schneider 2001). Ultimately, the hierarchical patch dynamics paradigm (HPDP) was proposed in 1995 (Wu and Loucks). It provided a more explicit conceptual framework that clarified and expanded upon some of Watt’s pioneering work; effectively linking complex systems theory, hierarchy theory, and patch dynamics with the principles of landscape ecology (Gillson 2004).

Before we explain HPDP in more detail, it is necessary to address some terminological discrepancies between two phrases sometimes used interchangeably with spatial scale. *Spatial resolution* and *spatial extent* often convey different or even conflicting meanings in the literature, thus warranting explicit definitions (Dungan *et al.* 2002). In this paper, we define spatial resolution as the level of detail or spatial resolution of a dataset (e.g., 30 m digital elevation model) (Turner *et al.* 1989), and spatial extent as the functional geographic area of respective abiotic or biotic phenomena (e.g., biotic influences from positive feedback mechanisms are most relevant at dozens or hundreds of hectares and climatic influences at tens of thousands of hectares) (Dungan *et al.* 2002). We recognize that spatial extent can also refer to the selected geographic area or boundaries of a study site and that ecological insight may be influenced by changing this extent as well, but we are not concerned with that in this paper.

In HPDP, similar to hierarchy theory, it is asserted that ecosystems are inherently complicated juxtapositions of nonlinear systems and sub-systems interacting across a dynamic environment within the confines of spatial and temporal heterogeneity (Gillson 2004). Ecological feedbacks and threshold responses predominate in these systems and sub-systems, enhancing the complexity. Ecological changes induced by varying heterogeneous processes occurring over periods of time are recognized at the meteorological, ecological, and geological temporal scales; which has been widely studied and accepted by ecologists (e.g., Davis et al. 2005; Taylor 2005; Brook and Bowman 2006). However, the primary emphasis in HPDP is placed on patchy mosaics of abiotic and biotic ecological hierarchies interacting to influence vegetation patterns on a landscape at various spatial extents (Wu and Loucks 1995). In essence, HPDP argues that unique combinations of abiotic and biotic ecological processes may be more influential in producing observed vegetative patterns of a particular geographic area at local, regional, or global scales; and that the combination of these effects generate patterns of vegetation on a landscape (Figure 6-1).

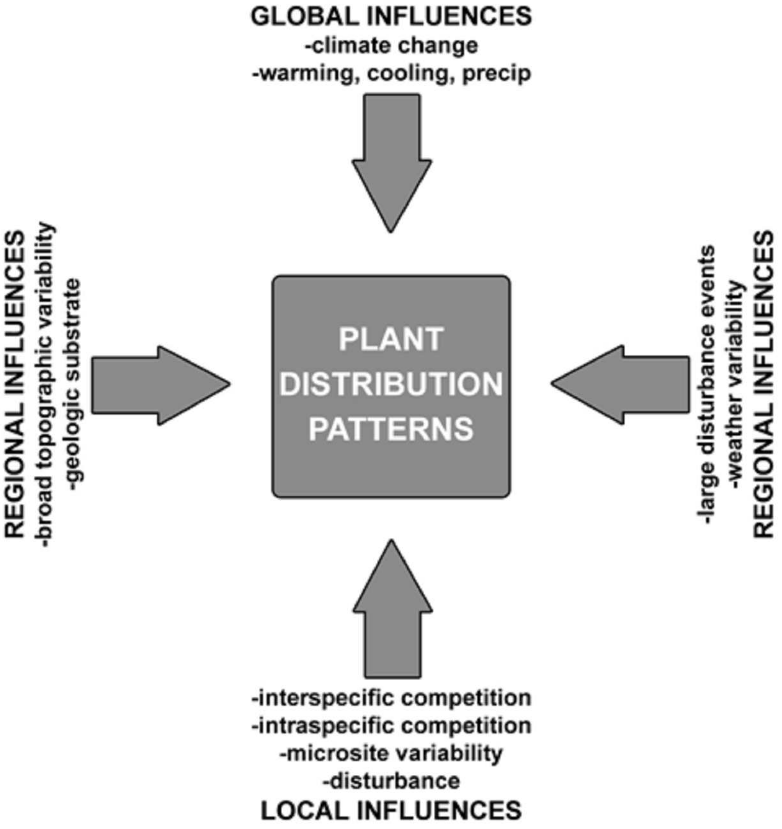

Figure 6-1: HPDP conceptual diagram depicting how various processes might interact at different spatial extents to influence plant distribution patterns. Ecologists have been cognizant of these potential influences for several decades (e.g., Watt 1947), but identifying and explaining what happens between the boundaries of ecological processes operating at different spatial extents and the corresponding influence of spatial resolution is a persistent challenge.

HPDP also recognizes that the selected spatial resolution of data utilized for conducting a particular study (such as tree establishment at treeline) may only best capture or represent a portion of the relevant ecological processes operating at a given spatial extent (Wiens 1989; Dungan *et al*. 2002) (Figure 6-2). For example, ecologists usually derive slope aspect from a digital elevation model (DEM) and utilize it as a surrogate for solar radiation, which exhibits a strong influence on spatial patterns of high-altitude tree establishment in mountainous regions (Holtmeier 2003). They typically map tree locations from the field and/or aerial photography, extract corresponding slope aspect values from a DEM, conduct multivariate statistical tests, and discuss the significance of the observed relationships (e.g., Stueve et al. 2009). However, the spatial resolution of the DEM used to calculate slope aspect and other variables may change how the analysis fits into the hierarchy of ecological processes controlling tree establishment (Figure 6-2). Fine-resolution DEM data (e.g., 2 m or less) captures microtopographic variability on generally exposed (e.g., south-facing) and sheltered (e.g., north-facing) slopes in the northern hemisphere (i.e., patches of slope aspect can be identified). Under this scenario, localized patches of north-facing slopes may occur on broad south-facing slopes and vice versa (Figure 6-3). Conversely, coarse-resolution DEM data tends to generalize microtopographic variability and portray the effects of solar radiation from a broader perspective (Figure 6-3). Depending upon the study area and influences from other processes, it is conceivable that the significance of slope aspect could be more or less important in controlling tree establishment patterns at either fine or coarse spatial resolutions.

Many ecological studies are performed using data with a specified spatial resolution so it is difficult to address and discuss (e.g., comparative analyses) empirical examples of the aforementioned concepts (e.g., Davis & Goetz 1990; Brown 1994b; Heyerdahl *et al.* 2001; Brook & Bowman 2006; Kumar *et al*. 2006; Bader *et al.* 2008). However, HPDP provides the necessary conceptual framework and rationale to understand how the selected spatial resolution of the data may be sensitive to ecological processes operating at different spatial extents. Unknown relationships between the spatial resolution of data used in a study and the spatial extent of ecological processes influencing spatial patterns in plant communities have the potential to change statistical inferences and corresponding theoretical implications in ecological research, which could also sway corresponding management strategies and policy development (Wu and Loucks 1995). HPDP can conceptually explain these relationships, but there is a dearth of supportive empirical reserarch (Gillson 2004). In trying to convey his perception of plant communities, Watt (1947) harkened back to a popular phrase from T. S. Eliot: "*we must know all of it in order to know any of it"*. To follow Watt's perception, it must be necessary therefore to investigate these unknown relationships between spatial resolution and extent in plant communities.

Most ecological research pertaining to HPDP involves conceptual explanations and potential applications in ecology, and only a limited quantity has empirically tested for the presence of HPDP and/or used HPDP to explain ecological patterns and processes (Gillson 2004). Two recent studies used HPDP to investigate tree abundance and patterns in African savannas. In Kenya, Gillson (2004) used palaeoecological techniques of fossil pollen and stable carbon isotopes to show that different ecological processes influence the spatial distribution of trees at micro, local, and landscape scales; thus providing empirical evidence of HPDP. She suggests that competing theories explaining savanna vegetation are not necessarily mutually exclusive (i.e., disturbance control versus plant-plant interactions); rather that they are equally important and may be interacting together in a structured hierarchy over space and time. In Namibia, Wiegand et al. (2005, 2006) used field surveys of bush, grass, and soil patterns along a steep rainfall gradient to demonstrate that tree distribution patterns are largely dictated by highly variable rainfall patterns and inter-tree competition interacting across the spatial mosaic of the landscape; thus concurring with the HPDP conceptual model. They

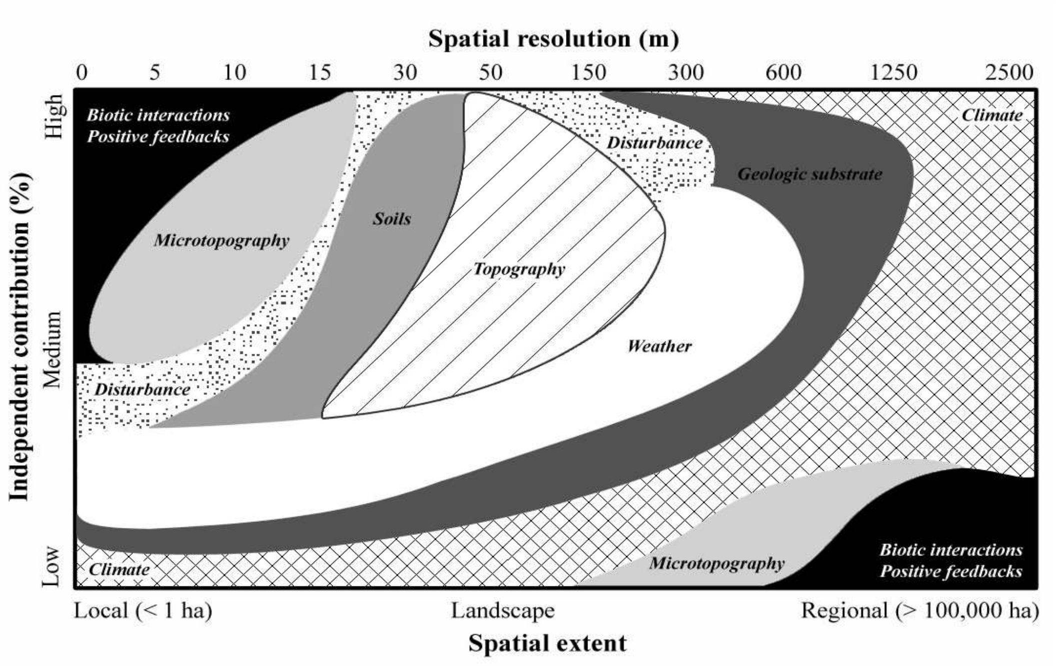

Figure 6-2: A conceptual representation of processes that control tree establishment at alpine treeline throughout various spatial extents and the consequences of using data with a select spatial resolution to examine the data with multivariate statistics. Independent contribution refers to the inferred statistical importance of an independent variable in influencing vegetation patterns.

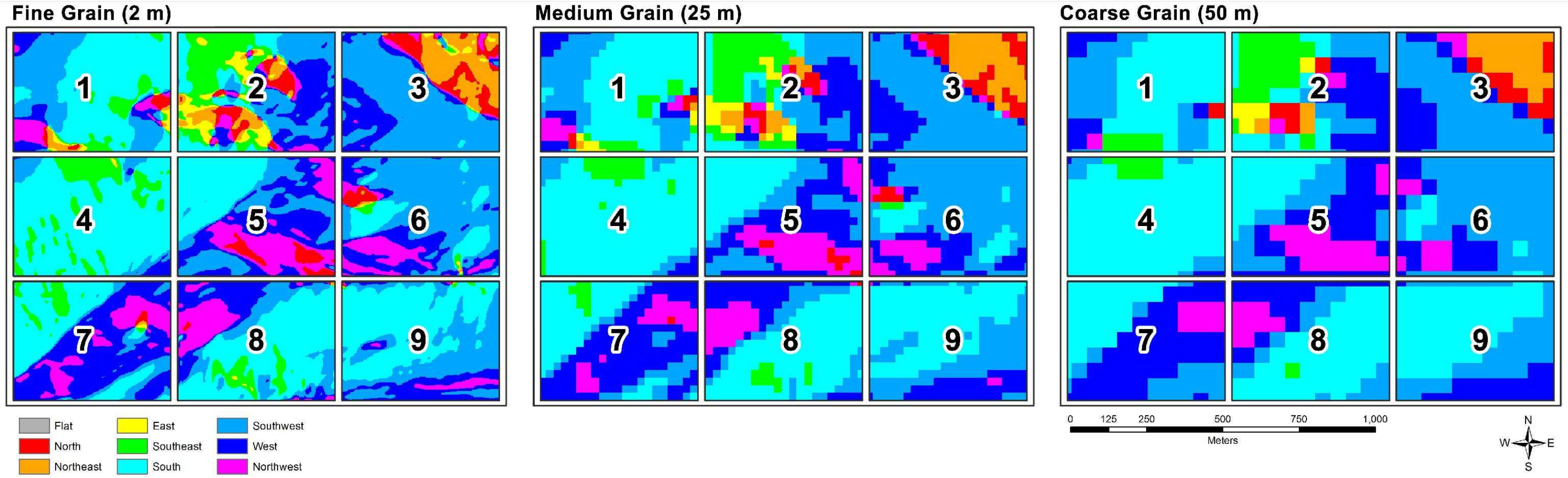

Figure 6-3: The influence of spatial resolution on derivations of slope aspect in the rugged mountainous environment of Mount Rainier (Stueve et al. 2009). We used a LIDAR-based DEM to derive slope aspect at 2 m and bilinear resampling allowed us to degrade the DEM to 25 m and 50 m. Note how microtopographic slope aspect features are blurred, and in some cases completely disappear, between fine (2 m) and coarse (50 m) spatial resolutions. This is particularly evident in grids 1, 2, and 3 where some south- and north-facing slopes are no longer apparent at a spatial resolution of 50 m.

asserted that either rainfall or inter-tree competition may appear most important at a particular study site, but both are probably equally important and structured hierarchically across the landscape. Scaling dependencies related to spatial resolution and extent have been reported in previous treeline studies (e.g., Walsh *et al*. 1994; Lawrence & Ripple 2000; Bruun *et al*. 2003; Walsh *et al.* 2003; Stueve et al. 2009), but these studies do not provide a comparative analysis of empirical evidence within the context of HPDP.

Treeline represents the ecotone between montane forests at lower elevations and alpine tundra at higher elevations (Holtmeier & Broll 2005). The transition may be abrupt (e.g., 10 m or less) or gradual (e.g., 100 m or more) and may or may not include krummholz form trees (i.e., stunted and short trees with twisted branches) (Figure 6-4) (Holtmeier 2003). Treeline environments provide an ideal scenario to test for the presence of hierarchical patch dynamics because abiotic and biotic variables (i.e., local site conditions) in topographically-complex mountainous environments usually interact to control tree establishment patterns at a broad range of spatial scales (Holtmeier & Broll 2005; Stueve et al. 2009). Furthermore, the boundaries separating the influences of local site conditions may change abruptly in treeline environments; sometimes varying over several meters or less (Holtmeier 2003). Explaining tree establishment patterns at treeline within the context of HPDP may also clarify whether abiotic or biotic influences are most important in influencing establishment patterns, or that both are structured hierarchically and equally important. A wealth of seemingly contradictory research has been performed over the last two decades concerning abiotic and biotic controls on tree establishment patterns. Some emphasizes the importance of the abiotic setting (especially elevation) (e.g., Brown 1994a; Brown 1994b; Walsh et al. 1994; Cairns 2001) and others the biotic setting (especially positive feedbacks associated with proximity to existing trees) (Malanson 1997; Smith et al. 2003; Alftine & Malanson 2004; Bekker 2005). Increased seed dispersal near sexually mature trees and the ameliorating effects of existing trees on the surrounding environment are thought to increase the importance of the biotic over the abiotic setting (Smith et al. 2003; Bekker 2005). Explaining tree establishment patterns at treeline within the context of HPDP may help reconcile these apparent discrepancies and provide better context for future research.

In this vein, we used aerial and satellite remote sensing, GIScience, and multivariate statistics to determine whether HPDP is present at treeline, and whether it can enhance explanations of post-fire tree establishment patterns at treeline. We asked what abiotic and biotic local site conditions were most important in dictating tree establishment patterns at various spatial resolutions (between 2 to 50 m at 2 m intervals) at a treeline disturbed by fire in Mount Rainier National Park. We reasoned that any variability in importance might suggest influences from hierarchical patch dynamics (e.g., abiotic and biotic controls operating at different spatial extents). We suspect the biotic surrogate (proximity to existing trees) will be most important at fine spatial resolutions and elevation at coarse spatial resolutions. We expect this because the fine spatial resolutions will likely be fully capable of capturing the environmental variability

Figure 6-4: *Abies lasiocarpa* (krummholz form) at treeline on the western slope of Mount Rainier, WA, USA.

associated with large and small patches of existing trees, thus highlighting steep gradients associated with establishment patterns and proximity to existing trees. However, this effect will probably be generalized and almost inconsequential at coarse spatial resolutions; ceding to the broad control of elevation changes. It is difficult to offer a hypothesis for the remaining variables beyond predicting that their importance will likely change between fine and coarse spatial resolutions.

6.2 Methods

6.2.1 Study site

Mount Rainier National Park is located on the western slope of the Cascade Range approximately 100 km southeast of Seattle, WA. The park was established on March 2, 1899 and is the fifth oldest national park in the U.S.A. Many ecologists have studied vegetation dynamics in the park over the last 110 years (e.g., Taylor 1922; Franklin *et al.* 1971; Hemstrom and Franklin 1982; Rochefort and Peterson 1996; Stueve et al. 2009). Treeline is generally between 1500 -2200 m a.s.l. Heavy annual snowfall from a pronounced orographic effect tends to depress treeline on the windward (western) side of Mount Rainier compared to the east. This study was conducted at a 150 ha treeline site disturbed by fire (in 1930) on the western slope of Mount Rainier. The altitude at the site ranges between approximately 1400-1800 m a.s.l. A substantial upslope pulse of tree establishment has been observed at the site after 1970. Additional information concerning the site is available from Stueve et al. (2009).

6.2.2 Data acquisition and processing

We used a 1970 CORONA (~1.9 m) satellite image and 2003 USGS DOQQ (1.0 m) to map 33 years of treeline change. Stueve et al. (2009) describe the processing of these data. Trees were mapped in each image by employing a binary classification of pixels with and without trees. Pixels that remained treeless between 1970 and 2003 were identified in addition to pixels in which trees had established themselves after 1970 and still persisted in 2003 (i.e., pixels that contained trees in 1970 and 2003 were excluded). These pixels served as the dependent variable in logistic regression analyses.

A LIDAR-based DEM (~1.8 m), ancillary climate data (i.e., direction of prevailing wind), and pixels identified as having trees in 1970 relative to those pixels in which trees became established after 1970 were used to derive the independent variables (Stueve et al. 2009). We used a processed bare-ground model DEM (tree tops removed) to extract elevation values and derivations of slope aspect and slope angle for each pixel using contextual data from the eight surrounding pixels in each case. We derived snow potential (i.e., depth of winter snowpack) from southwesterly prevailing winds and topographic variability modeled using the DEM (e.g., leeward and concave slopes are more likely to contain persistent snowpack versus windward and convex slopes) (Frank 1988; Burke *et al.* 1989; Brown 1994b). We also used the DEM to model topographic variability and derive the wetness potential (e.g., concave depressions with large upslope catchment areas are more likely to be wet versus convex slopes with a limited upslope catchment areas) (Beven & Kirkby 1979; Brown 1994b) and erosion potential (e.g., enclosed topographic concavities with limited upslope catchment areas are less susceptible to erosion than ravines and streams with large upslope catchment areas) (Moore *et al.* 1993). We used Euclidean distance to measure proximity to 1970 trees (hereafter, proximity to trees) with pixels classified as trees in 1970 serving as the starting points. We derived direction from 1970 trees (hereafter, direction from trees) from the same pixels as proximity to existing trees (e.g., identified pixels as being on the N, NE, E, SE, S, SW, W, or NW side of trees that existed in 1970).

Stueve et al. (2009) reported spatial preferences for post-1970 tree establishment at the site: those are close proximity to 1970 trees (< 50 m), at elevations between 1250-1350 m a.s.l., on moderate (40-60°) slopes, at sheltered (W-, NW-, N-, NE-, and E-facing) sites, in relatively xeric conditions, on protected sides of 1970 trees (NW, N, NE), and at sites with intermediate snowpack.

6.2.3 Scaling spatial resolution and sampling procedures

Simulations of progressively broader influences from local site conditions that represent the potential presence of hierarchical patch dynamics were achieved using digital image resampling. We used bilinear interpolation to resample all the local site conditions to between 2 and 50 m at 2 m intervals (Jensen 2005). With this procedure, the weighted values of the four nearest input cells are used to calculate the value of the output cell. We ceased resampling at 50 m because continuing the process would have necessitated a decrease in the number of our sample points to a point where it compromised statistical rigor. In addition, we used the nearest neighbor method to resample mapped areas of tree establishment to 2 m (i.e., to match the 2 m starting point of the independent variables) (Jensen 2005). The original cell values of the input image are maintained with this method and the output cell values are dictated by the nearest neighbor of the input cells.

The 2 m binary image of mapped tree establishment was continually used as the dependent variable in an effort to represent fine-resolution data commonly collected from the field or aerial photography in ecological studies. Successively coarser local site conditions served as independent variables (i.e., 2 to 50 m at 2 m intervals) to encompass the range of widely available digital elevation models (e.g., 10 m USGS, 30 m USGS, and 50 m GSI (Japan)) commonly used in ecological studies and also to represent ecological processes operating at disparate spatial extents. It was important to maintain the dependent variable at a spatial resolution of 2 m because matching it with the spatial resolution of the successively changing independent variables would have resulted in large pixels being classified as trees when, in fact, the area encompassed by them might include significant amounts of tundra or rock.

Two hundred randomly generated points were created from the 2 m dependent variable with logical restrictions that prevented more than one point from occupying similar cells in the independent variables. Each point was sampled at 2 m intervals. At each interval, we extracted data from both the independent and dependent variables for specific *x* and *y* coordinates that corresponded to the 200 sample points, and applied logistic regressions to all points. We extracted 200 points in order to ensure statistical rigor and avoid having sample points placed in the same cells when increasing the spatial resolution to 50 m.

6.2.4 Statistical analyses

Techniques utilized by Stueve et al. (2009) were used to rank the individual importance of each of the independent variables for every 2 m increment and test the null hypothesis that tree establishment patterns are not controlled by local site conditions (i.e., they are random). The data exhibited some signs of multicollinearity (i.e., some pairs of independent variables approaching correlation coefficients of 0.7), which made us concerned that traditional regression techniques would not provide reliable rankings (Mac Nally 1996). Hosmer and Lemeshow (2000) advise against using traditional logistic regression with correlation coefficient values approaching 0.7 and others recommend a threshold of 0.5 (Hessl & Baker 1997). Thus, we used *R 2.4.1 (2006)* to conduct logistic regressions within the hierarchical partitioning framework (i.e., *all.regs* and *hier.part* functions) (Chevan and Sutherland 1991; Mac Nally 1996). This approach mitigates the effects of multicollinearity and considers all possible combinations of influences from the independent variables (Mac Nally 1996). The cumulative explanatory power derived from this approach tends to be substantially lower than those using cumulative R^2 associated with traditional regression approaches because joint contributions are excluded (Mac Nally 1996). Dependent variables for all regression sequences were recoded to 0 and 1. We removed all outliers and used mathematical functions (i.e., logarithmic and square root) to reduce skewness and kurtosis. The randomization approach was used to obtain Z-values and assess the significance of each independent variable (Mac Nally 2002). We also calculated the range of confidence intervals for all independent variables to determine if their rankings were statistically different (i.e., no overlap between ranges).

To prevent the potentially erroneous rankings of independent variables (Griffith *et al.* 2006), we modeled spatial autocorrelation for the study site with a modification of the principal coordinates of neighbour matrices approach (Dray *et al.* 2006). A spatially-weighted landscape matrix was generated using a Delaunay triangulation, which was selected as the most suitable approach in data-driven Akaike information criterion rankings. The resulting matrix provided continuous data that respectively quantified positive and negative spatial autocorrelation and was incorporated as an additional independent variable in the regression analyses (Griffith *et al.* 2006).

6.3 Results

6.3.1 General trends

For all spatial resolutions, we were able to reject the null hypothesis and accept the alternative hypothesis that tree establishment patterns are controlled by local site conditions (i.e., not random) (Figure 6-5). The relationship between the statistically important local site conditions is clearly tiered. Proximity to trees and elevation rival each other and explain the highest proportion of the variance across all spatial resolutions (Figure 6-5). There is a large gap before the second most important cluster including slope angle, slope aspect, and direction from trees is evident (Figure 6-5).

Proximity to trees, elevation, slope angle, and slope aspect were consistently the most influential local site conditions, but they exhibited a slight decrease in cumulative importance with increasingly coarse spatial resolutions (Figure 6-5). Their independent contributions explained nearly 28% of the variation in tree establishment patterns at 2 m before tapering to slightly above 21% at 50 m. We originally excluded direction from trees from Figure 6-5 because it was marginally important at fine spatial resolutions. However, it displayed a sharp increase in importance at coarse spatial resolutions approaching 50 m (nearly six times greater than the value at 2 m) and thus we included it. The remaining local site conditions (i.e., wetness potential, snow potential, and erosion potential) all maintained similar, but less pronounced, cumulative importance across the range of spatial resolutions that hovered around 0.5%. These variables exhibited minimal changes with marginal statistical significance (i.e., 95% confidence level) and thus, are not addressed further.

6.3.2 Individual trends

Between spatial resolutions of 2-30 m, the ranked importance of local site conditions in descending order was proximity to trees, elevation, slope angle, slope aspect, and direction from trees. All were significant at the 99% confidence level except for direction from trees. The degree of separation between these variables remained relatively constant until about 16 m. Subsequently, proximity to trees and elevation in addition to slope angle, slope aspect, and direction from trees slowly conflated toward 30

m. Near 30 m, the variance explained by proximity to trees began to plummet and elevation started to ascend.

Likewise, the variance explained by slope angle declined sharply while slope aspect and direction from trees steadily increased near 30 m. After 40 m, the variance explained by elevation fully supplanted proximity to trees. The importance of slope aspect and direction from trees also surpassed slope angle. At this juncture, all variables remained significant at the 99% confidence level except for slope angle. By 50 m, the ranked importance in descending order was elevation, proximity to trees, direction from trees, slope aspect, and slope angle. The first four variables remained significant at the 99% confidence level, but slope angle was only marginally significant (95% confidence level).

6.4 Discussion

HPDP theorizes that multiple abiotic and biotic processes interact in a structured hierarchy at disparate spatial extents to influence vegetation dynamics and observed patterns of vegetation in the patch-corridor-matrix (Wu and Loucks 1995; Gillson 2004). Some of these processes may operate locally at confined spatial extents (e.g., interspecific plant interactions at ecotones) or regionally/globally at broad spatial extents (e.g., weather and climate). Because these processes are scale-dependent, changes in the spatial resolution used to analyze vegetation communities may increase or decrease the importance of a variable in controlling vegetation patterns. Sometimes these changes in

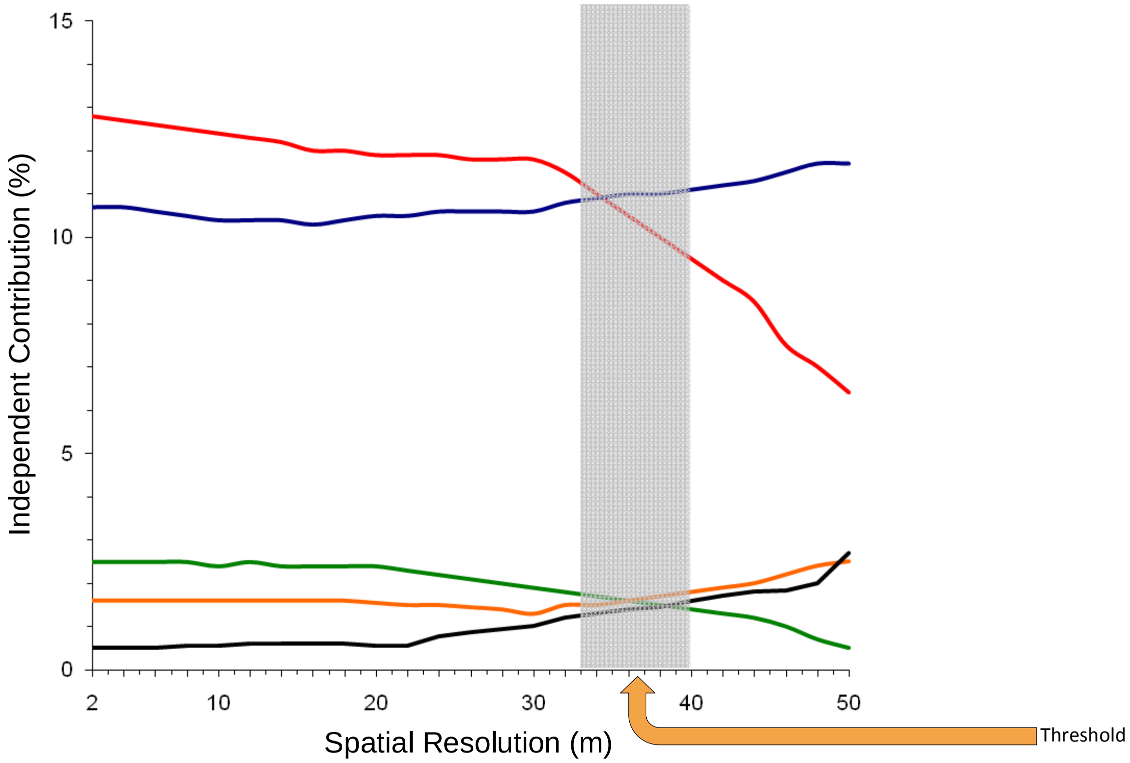

Figure 6-5: Ranked order of the five most important local site conditions as inferred from logistic regression in the hierarchical partitioning framework. The local site conditions were resampled and tested at 2 m intervals, commencing at 2 m and terminating at 50 m. Red = proximity to 1970 trees, blue = elevation, green = slope angle, orange = slope aspect, and black = direction from 1970 trees. Note that direction from trees was included because its importance increased substantially when approaching a spatial resolution of 50 m. The rankings of proximity to 1970 trees and elevation are insignificant at ~32-37 m. The rankings of the other three variables are insignificant at ~31-41 m. The rankings of direction from 1970 trees and slope aspect remain insignificant up to 50 m.

relative importance are incremental and may not influence the results, but in other cases change is rapid and thresholds are crossed. Conceptually, these assertions are understood well. Thus, it also seems logical to conclude within the context of HPDP, that using varying spatial resolutions of data to represent abiotic and biotic local site conditions may introduce some uncertainty due to ecological processes operating at different spatial extents (e.g., interspecific interactions between plants are more important than climate and weather at fine resolutions). Remarks concerning scaling dependencies in the peer-reviewed literature provide some evidence of the aforementioned concept, but these papers lack the theoretical underpinnings of HPDP (e.g., Dullinger et al. 2003b; Huete et al. 2005).

Four characteristics of the results presented here appear to provide empirical evidence for the presence of hierarchical patch dynamics. First, as might be expected with the presence of hierarchical patch dynamics, proximity to trees supersedes the importance of all local site conditions at finer spatial resolutions. Proximity to trees is an excellent biotic surrogate for positive interspecific plant interactions (e.g., ability of trees to modify their surroundings) and seed dispersal (e.g., higher seed density near existing trees) when pulses of increased tree establishment have been documented (Bekker 2005; Dickie et al. 2005; Stueve et al. 2009). This strong positive ecological inertia of trees is highlighted quite well at finer spatial resolutions. For example, in this case, detailed distances between small patches of trees can be more readily denoted and the cumulative effect of this data may obscure the potential importance of other variables (Figure 6-6). Nevertheless, several abiotic variables remain statistically significant.

Secondly, an interesting transition in the ranked importance of local site conditions appears at moderately coarse spatial resolutions (i.e., ~35 m). This indicates that important ecological thresholds or boundaries exist where the influence of abiotic and biotic processes operating at different spatial extents changes quickly. This further supports HPDP and concepts of structured hierarchies of abiotic and biotic processes operating with sharp, well-defined boundaries.

Thirdly, elevation emerges as the most significant independent variable at coarser spatial resolutions beyond the aforementioned threshold. Elevation is a classic abiotic surrogate for temperature change and widely found to be important in controlling tree establishment at both disturbed and relatively undisturbed treelines (e.g., Tranquillini 1979; Körner 1998; Stueve et al. 2009). Temperature changes associated with elevation

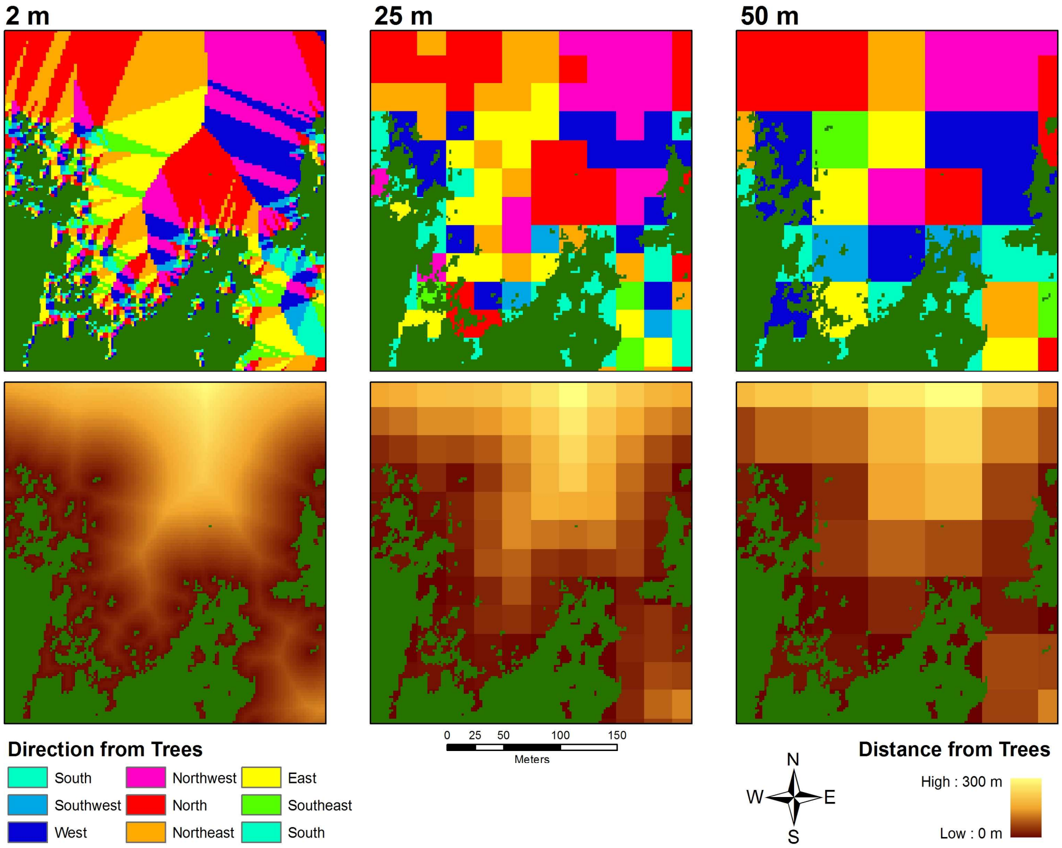

Figure 6-6: Snapshots of direction from 1970 trees (top) and distance from 1970 trees (bottom) at 2, 25, and 50 m over a small portion of the study site. Green areas denote trees present in 1970 as detected by the CORONA satellite photography.

are likely less pronounced at finer spatial resolutions (i.e., less likely to have variability between pixels) whereas proximity to existing trees or some other biotic factor may be more important. However, at coarser spatial resolutions, the broader influence of temperature change will likely be more pronounced and exceed the importance of localized biotic factors. Positive feedback effects rarely extend more than a couple dozen meters beyond existing trees, and the ground coverage of seed dispersal rapidly declines with distance from existing trees (Coop and Givnish 2007; Stueve et al. 2009). The comparatively coarser pixels likely generalize the effects of positive biotic interactions and seed dispersal detected at finer resolutions, further accentuating thermal differences corresponding with altitudinal variability. This continues to build support for HPDP.

Finally, the independent variables of direction from trees, slope angle, and slope aspect exhibit discrepancies in importance between fine and coarse spatial resolutions. This is similar to the situation with proximity to trees and elevation, lending additional credence to HPDP. At finer spatial resolutions, direction from trees is denoted for individual trees, clusters of small tree patches, and large patches of trees (Figure 6-6). The ameliorating effects of protected edges (i.e., northerly side of trees or tree patches) probably facilitates establishment in these areas. However, at coarser spatial resolutions, this effect is probably accentuated because some areas previously classified as exposed (i.e., southerly side of trees) on the fine-scale maps are generalized to a protected classification (e.g., a series of tree patches on the north side of a large patch of trees) on the broad scale maps (Figure 6-6). In terms of slope angle, fine-scale variability is probably more important in dictating soil development (especially steep slopes) and illuminating competitive influences from herbaceous cover (especially gentle slopes) (Figure 6-7). Conversely, exposure on south-facing slopes matters less at finer scales and is more important at coarser scales that denote generally south- versus north-facing ridges (e.g., microtopographic south-facing slopes on a broad north-facing ridge have less influence on tree establishment) (Figure 6-7).

Hierarchical patch dynamics appears to be influencing tree establishment patterns at this disturbed treeline and introducing variability in corresponding multivariate

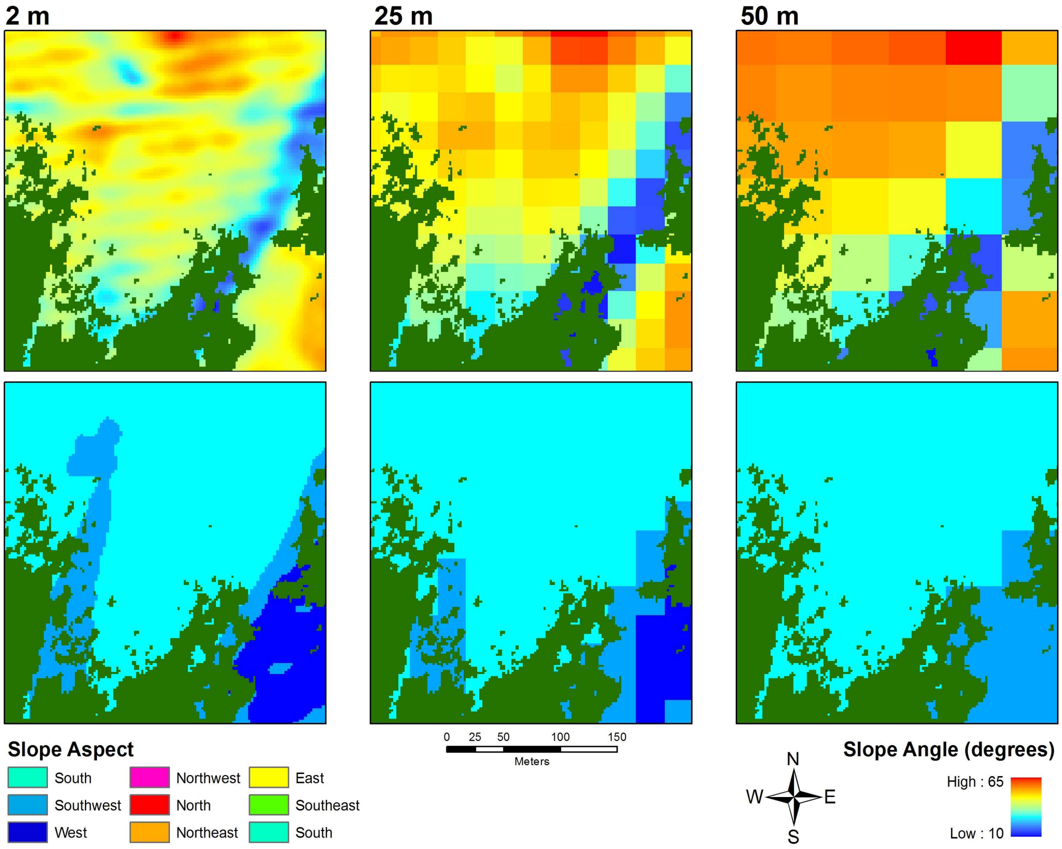

Figure 6-7: Snapshots of slope angle (top) and slope aspect (bottom) at 2, 25, and 50 m over a small portion of the study site. Green areas denote trees present in 1970 as detected by the CORONA satellite photography.

statistical analyses. Independent assessments of the same study site could have produced conflicting results with merely a subtle change in the spatial resolution used for the independent variables. For instance, positive feedback associated with proximity to trees (biotic variables) is most important from 2-32 m, conversely, shortened growing seasons and temperature changes associated with elevation (abiotic variable) is most important from 37-50 m. This is a crucial issue, especially when considering the importance of using inferences from multivariate statistics in formulating ecological theory and in making critical management or policy decisions. Thus, it appears that both the biotic (positive feedbacks) and abiotic (elevation) setting are equally important in controlling tree establishment at treeline. Discrepancies in their importance probably exist because these variables are hierarchically structured in alpine landscapes.

6.5 Conclusions

Research conducted at a particular spatial resolution is not necessarily erroneous and there probably is not an optimum or ‘best’ spatial resolution. Rather, we argue that a range of spatial resolutions should be explored within the context of the question(s) being addressed. It would be a worthwhile pursuit to examine how the relationships between ecological patterns and processes in the patch-corridor-matrix vary with the spatial resolution of analysis in a multitude of ecosystems. Critical thresholds may be identified where the importance of independent variables in controlling some ecological process and/or patterns changes (e.g., ~35 m in this study). Understanding the relationships between various ecological patterns and processes operating at different spatial extents, and the spatial resolution of analysis, is of paramount importance to advancing ecological thought. Furthermore, the additional insights will complement previous research, provide a broader perspective on more contemporary research, and enhance our understanding ecosystem structure and function**.** Therefore, we argue that ecologists should explicitly address and empirically test for hierarchical patch dynamics in future research.

CHAPTER VII

INTERPRETATIONS AND CONCLUSIONS

Biogeographers and ecologists seldom conduct their research in a controlled setting, particularly during applications of landscape-scale research. Additionally, a digital GIS environment usually represents the 'reality' of the respective study site and sparse temporal coverage of remote sensing platforms in rugged terrain may limit the ability to thoroughly represent the landscape. Thus, this usually necessitates accepting certain assumptions and maintaining an awareness of the potentially confounding influences of external factors when interpreting the results. Chapter VII offers a synopsis of the research presented in this dissertation while also considering any assumptions and influences of external factors (Section 7.1), before finishing with some concluding thoughts (Section 7.2).

7.1 Summary

The primary objectives of this dissertation (c.f. Section 1.3) were to map treeline vegetation and local site conditions, assess and explain structural changes of arboreal treeline vegetation, compare different statistical approaches when assessing the structural changes of arboreal treeline vegetation, and test for the presence of hierarchical patch dynamics. In this section, I revisit these objectives, and discuss two assumptions and three limitations relevant to the achievement of the objectives.

7.1.1 Mapping procedures

Sometimes, it can be challenging to classify and georeference aerial photographs with a high spatial resolution in mountainous terrain, but that was not the case here. Orthorectification enabled the proper alignment of mapped vegetation data in a projected space with an RMSE below 0.5 pixels. Previous published studies that used temporal composites of remotely sensed data in a similar fashion (e.g., examining treeline or subalpine forest in mountainous terrain) failed to do this (e.g., Carmel & Kadmon 1999; Cushman & Wallin 2000; Hoersch et al. 2002; Klasner & Fagre 2002; Butler et al. 2003). Thus, this dissertation represents a marked improvement in the data inputs over these studies. It also demonstrates that historical photography from mountainous terrain may be properly and confidently analyzed in a GIS environment to address biogeographic research questions. Additionally, the fitted modal filter and exposed south-facing slope of the large ridge at the study site allowed for a high degree of accuracy in the binary classifications of the photographs (i.e., near 90%). It was also advantageous having a LIDAR-based DEM with a fine spatial resolution to match up with the fine-scale aerial photographs. Ultimately, I remain very confident in the ability of the accurately mapped fine-scale data to allow the statistical, structural, and hierarchical questions be adequately addressed in Chapters IV, V, and VI.

7.1.2 Statistical comparisons

Problems associated with multicollinearity between independent variables are sometimes challenging for biogeographers and ecologists to address (Mac Nally 2002). This is an especially noteworthy concern in treeline environments because independent variables tend to be highly correlated (Brown 1994b; Stueve et al. 2009). In demonstrating the potentially confounding influence of correlated independent variables, it was very useful to apply a nonstandard hierarchical logistic regression application to the data and compare it with the traditional approaches in Chapter IV. This allowed me to compare and contrast the different approaches, and sufficiently convey the ramifications of selecting the proper or improper statistical approach; so much so, that one might question the continued use of the traditional approaches in treeline environments. This comparative insight enhanced interpretations of structural treeline changes in Chapter V and hierarchical patch dynamics in Chapter VI. Specifically, the dominant influence of proximity to trees would have been discounted without examining the alternative approach and comparing it with the traditional approach.

7.1.3 Controls on spatial patterns of tree establishment

The abiotic setting has received a considerable amount of attention from biogeographers and ecologists attempting to explain tree establishment controls at treeline over the last two decades (e.g., Brown 1994b; Walsh et al. 1994; Cairns 2001;

Bian & Walsh 2005). In Chapter V, sharp changes in landscape heterogeneity identified by the contagion index indicated that tree establishment patterns were being controlled by various local site conditions. I was able to apply a hierarchical logistic regression approach to mitigate the effects of multicollinearity and identify a biotic factor (proximity to existing trees) as the most important control on tree establishment when considering the entire study area. This biotic factor remained important at restricted spatial extents near the forest line and only relinquished importance to the abiotic setting with increased distance upslope from the forest line. This intriguing finding will likely stimulate additional studies at undisturbed treelines to see if similar patterns prevail. It suggests that the assumption of treeline vegetation being in equilibrium or quasi-equilibrium with the surrounding abiotic environment is not reasonable.

7.1.4 Hierarchical patch dynamics

Biogeographers and ecologists have long been aware of the influences of spatial scale and hierarchies of ecological processes when conducting research (e.g., Watt 1947). Some of these issues have also surfaced in treeline research; loosely referred to as scaling dependencies (e.g., Walsh et al. 1994). In Chapter VI, I was able to exploit the fine spatial resolution of the LIDAR-based data, 2003 aerial photography, and 1970 CORONA photography to document continuous changes in the importance of tree establishment controls from fine grains (2 m) to coarse grains (50 m). Proximity to existing trees was most important at fine grains and elevation was most important at coarse grains. The importance of additional abiotic variables such as slope aspect, slope angle, and direction from 1970 trees also changed between fine and coarse grains. This appears to provide at least circumstantial evidence for the presence of hierarchical patch dynamics. At the least, it identifies potential pitfalls for biogeographers and ecologists when conducting research at treeline.

7.1.5 Assumptions

I placed parts of this dissertation in the context of the treeline ecotone literature. However, in an effort to link their results with climate, many treeline studies intentionally avoid sites that are disturbed to avoid what is perceived to be potentially confounding influences from the disturbance (e.g., Cuevas 2002). I argue that disturbed treelines are equally useful to study because the upslope advancement of undisturbed treelines may remain impeded by similar interactions between local site conditions, despite the presence of increasingly favorable climatic conditions. Thus, the first crucial assumption of this dissertation is the following: the underlying mechanisms controlling tree establishment patterns at disturbed treelines are similar to those controlling relatively undisturbed treelines. Recent research conducted at an undisturbed treeline site in Denali National Park and Preserve indicates that this assumption may be reasonable (Stueve & Isaacs 2009).

A second assumption is that nominally classified raster-based cells are an adequate representation of reality. Some cells classified as trees contained tundra and vice versa. In 1970, 5.6% of the ground verification points were classified as treeless when, in fact, tree saplings were present. Similarly in 2003, 5.0% of the ground verification points were improperly classified in this manner. In each case, the small tree saplings were probably too small to be detected by the imagery. Alternatively, 14.9% of the ground verification points from 1970 and 17.4% from 2003 were erroneously classified as trees when they should have been treeless. Complications from tree shadows probably contributed to these errors. These errors provide less confidence in the order of closely ranked variables, but probably have little influence on the other rankings.

7.1.6 Limitations

One limitation is the number of images from representative decades incorporated in the temporal sequence of images documenting treeline changes at the study site. The analysis could have been more robust and far-reaching with the incorporation of at least one additional photograph from the 1930's, 1940's, or 1980's in order to establish a more thorough temporal sequence of data. However, the remote location of the study site limited the number of available photographs, and cloud cover and/or degraded photographs prevented the use of some data that could have expanded the temporal coverage.

A second potential limitation is the relatively small spatial extent of the study site (~150 ha). Expanding the analysis to include other disturbed and undisturbed treeline sites would have provided useful comparative data (e.g., windward versus leeward sides of Mount Rainier). However, the availability of the LIDAR-based data was restricted and adequate aerial photography was lacking. Most importantly, financial limitations and time constraints did not make the inclusion of additional sites feasible.

A third limitation is the nominal classifications of the treeline environment. Nominal classifications necessitate the use of logistic regression, which is less robust than multivariate normal regressions that use continuous data for both the independent and dependent variables. However, nominal classifications generally suffice and are regularly used for black and white aerial photographs (Jensen 2005). Fuzzy classifications that produce continuous data are not suited well to black and white photographs and it is impossible to do band ratios to produce continuous data with black and white photographs because they only contain one band.

7.2 Conclusions

The influence of proximity to existing trees was clearly a dominant force in controlling tree establishment patterns at this disturbed treeline. Importantly, it exceeded the influence of elevation and other abiotic variables at this study site. Even at restricted spatial extents and when changing spatial grain, proximity to existing trees persisted as an important factor that equaled or exceeded the importance of the abiotic setting. Only when considering independent variables with a spatial grain > 35 m or spatial extents several hundred meters upslope beyond the forest line did parameters describing the abiotic system begin to exceed the importance of proximity to existing trees. The dominance of proximity to existing trees at this site is in stark contrast to the importance of abiotic tree establishment controls in other treeline studies. This finding raises the question as to whether this site is unusual ecologically, or whether the statistical analyses undertaken provided new insights. If the latter, it may be useful to reexamine patterns of tree establishment at previously studied treeline sites to determine if they correspond with the results presented here. A similar analysis of structural treeline changes in a completely different landscape (ecologically and physiographically) over 1500 miles north of Mount Rainier also reported proximity to existing trees as the most important controller of tree establishment (Stueve & Isaacs 2009); thus indicating that the findings presented here may be salient beyond this south-facing ridge on the western slope of Mount Rainier.

The four following factors are probably responsible for biogeographers and ecologists and biogeographers identifying and reinforcing the importance of the abiotic setting in controlling tree establishment at treeline:

(1) A biotic factor was not considered and the use of traditional logistic regression enhanced the importance of the abiotic setting, which made abiotic influences appear overly strong.

(2) Plot-level studies established in the field were influenced by the spatial extent of processes operating in the treeline ecotone (i.e., they were established in the uppermost

portions of treeline where the abiotic setting may be slightly more important than the biotic setting).

(3) A biotic factor was included, but applications of traditional logistic regression and overly correlated independent variables minimized the importance of the biotic factor.

(4) Landscape-scale studies conducted at select spatial grains were positioned at places in the hierarchical level of ecological processes controlling treeline that are not as sensitive to the influences of biotic factors (e.g., the importance of proximity to existing trees might appear less important when using > 35 m pixels to assess a few decades of change).

The research presented in this dissertation ultimately suggests that the assumption of treeline vegetation being in equilibrium with the surrounding physical environment may not be reasonable. Although important, this point is probably inconsequential to those biogeographers and ecologists that accept non-equilibrium paradigms. However, it is crucial to others (i.e., predictive modelers) when equilibrium assumptions are often critical to the applicability of the models. Indeed, it appears that tree colonization in mountainous regions may largely resemble observed patterns on flat, forested landscapes where distance to viable seed sources is usually the most important factor controlling patterns of establishment. However, this insight would have been lost without performing an alternative logistic regression approach or considering hierarchical patch dynamics, and reaffirmed the importance of the abiotic setting. As it is, positive ecological inertia associated with close proximity to existing trees appears to exceed the importance of steep environmental gradients in the abiotic setting. That is, increased availability of seed and the ability of established trees to ameliorate their surroundings probably play pivotal roles in elevating the importance of proximity to existing trees. Indeed, it appears that Tobler’s (1970) first law of geography is alive and well at Mount Rainier: "Everything is related to everything else, but near things are more related than distant things."

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APPENDIX A

Manuscript Published in *Journal of Vegetation Science*

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Post-fire tree establishment patterns at the alpine treeline ecotone: Mount Rainier National Park, Washington, USA

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Abstract

Questions: Does tree establishment: (1) occur at a treeline depressed by fire, (2) cause the forest line to ascend upslope, and/or (3) alter landscape heterogeneity? (4) What abiotic and biotic local site conditions are most important in structuring establishment patterns? (5) Does the abiotic setting become more important with increasing upslope distance from the forest line?

Location: Western slopes of Mount Rainier, USA.

Methods: We performed classification analysis of 1970 satellite imagery and 2003 aerial photography to delineate establishment. Local site conditions were calculated from a LIDAR-based DEM, ancillary climate data, and 1970 tree locations in a GIS. We used logistic regression on a spatially weighted landscape matrix to rank variables.

Results: Considerable establishment after 1970 caused forest line elevation to increase over 150 m in specific locations. Landscape heterogeneity increased with distance from the 1970 forest line. At a broad spatial context, we found establishment was most common near existing trees (0-50 m) and at low elevations (1250-1350 m). Slope aspect (W, NW, N, NE, and E), slope angle (40-60°), and other abiotic factors emerged as important predictors of establishment with increasing upslope distance from the forest line to restricted spatial extents.

Conclusions: Favorable climatic conditions likely triggered widespread tree establishment. Readily available seed probably enhanced establishment rates near sexually mature trees, particularly in the less stressful environment at low elevations. The mass effect of nearly ubiquitous establishment in these areas may have obscured the importance of the abiotic setting to restricted spatial extents. Topographic variability apparently produced favorable sites that facilitated opportunistic establishment with increasing upslope distance from the forest line, thereby enabling additional trees to invade the alpine tundra.

Keywords: *Abies lasiocarpa*; CORONA; Hierarchical partitioning; Landscape; Pacific Northwest; Seed dispersal; Spatial autocorrelation; Subalpine parkland; Topography.

Abbreviations: DEM = digital elevation model; DOQQ = digital orthophoto quarter quadrangle; GIS = geographic information system; LIDAR = light detection and ranging.

Nomenclature: Anon. (1993).

Introduction

The alpine treeline ecotone (treeline) exhibits one of the most striking transitional physiognomic landscapes, which has garnered attention from vegetation scientists interested in assessing the floristic impacts of climate change (Walther 2003). Treelines often display remarkable variability in structure and composition between different regions, thus contributing to a wide range of definitions (Holtmeier 2003). Simply stated, the treeline demarcates the boundary between closed forests at low elevations and the alpine tundra at high elevations. In the Pacific Northwest, this boundary is characterized by a broad ecotone extending from closed canopy forest through subalpine parklands, to the scrub line or upper limit of trees (Franklin & Dyrness 1988). The subalpine parkland is comprised of a mosaic of tree clusters and herbaceous vegetation, often extending over an elevation gradient of 300-400 m. The upper limit of this zone is variable and may be composed of krummholz (German for short crooked trees) or upright arboreal vegetation.

The traditional paradigm contends that temperature controls altitudinal limits of treelines and that observed upslope advance is the most likely response to climatic warming (cf. Daniels & Veblen 2003). However, others caution that disturbances

(Daniels & Veblen 2003; Cairns & Moen 2004) and variability of tree responses to local site conditions (Miller & Halpern 1998; Holtmeier & Broll 2005) may confound interpretations, making any direct connections to climate tenuous. Reports of relatively stable treelines over the last 50 years warrant these concerns (e.g. Cuevas 2002; Klasner & Fagre 2002). The paucity of known relationships between disturbance events, climate, local site conditions, and altitudinal limits of treelines necessitates additional research to place observed treeline positions in a climatic context (Daniels & Veblen 2003; Holtmeier & Broll 2005).

Many treeline studies are intentionally executed at relatively undisturbed sites in an attempt to correlate results with climatic fluctuations and thus avoid what is perceived to be confounding influences from disturbances (e.g. Cuevas 2002). We assert that disturbed treelines are equally useful to study, given that upslope advance of treelines is often impeded by local site conditions, despite favorable climatic influences, and that some treelines are relicts of past climates (Holtmeier 2003; Lingua et al. 2008). Local site conditions that structure establishment patterns (i.e. spatial arrangement of newly established trees) at disturbed treelines may resemble those at relatively undisturbed sites. Thus, studying both can contribute to a better understanding of factors controlling treeline.

Fire is an important disturbance agent capable of destroying existing trees and depressing the altitudinal limits of treelines (Wilson & Agnew 1992; Noble 1993). Many studies have utilized field plots and dendroecology at local scales to assess treeline recovery after a fire event. Bollinger (1973), for instance, analyzed tree rings from the Colorado Front Range and concluded that fire suppresses treelines to new climatically controlled positions where recently established herbaceous cover inhibits treeline recovery. In the same study area, Peet (1981) argued that fire and climate cause treelines to exist in dynamic equilibrium, whereby treelines recover slowly after a fire event, with the highest rates of establishment occurring uniformly near existing trees. He predicted future fires would prevent treelines from reaching altitudinal limits controlled by climate. Shankman (1984) demonstrated that the Colorado Front Range treelines slowly established upslope after a fire disturbance, with the greatest recovery rates occurring at low elevations and in close proximity to existing trees. He posited that treelines could recover to their original altitudinal limits gradually and in a uniform manner, provided that there are no additional disturbances.

Additional studies have illustrated the importance of local site conditions. Agee & Smith (1984) determined that close proximity to patches of surviving trees and lack of deep snow cover were directly related to the highest rates of establishment after fire in the Olympic Mountains, Washington. In the Colorado Front Range, Shankman & Daly (1988) determined that topographically sheltered sites exhibited high rates of establishment after fire and predicted that the treeline would return to its pre-disturbed altitudinal position in a patchy manner. They also noted that a few topographically exposed sites having xerophytic tree species experienced increased rates of establishment. Noble (1993) developed raster-based models depicting interactions between fire disturbance, climate, and subsequent establishment at the treeline. He proposed that upslope treeline advance after fire would be episodic and exhibit heterogeneous establishment patterns.

Clarifying the importance of local site conditions in structuring establishment patterns at the treeline requires the use of a complex landscape ecological approach (Holtmeier 2003). We used satellite imagery, aerial photography, digital terrain data, and ancillary climate data in a GIS environment to explain landscape-scale patterns of establishment at a treeline disturbed by a 1930 fire in Mount Rainier National Park. We suspect that establishment and upslope advance of the forest line will be evident because climate has been generally favorable (i.e. warm and dry summers) throughout the 20th century, particularly on the western slopes of Mount Rainier (Rochefort & Peterson 1996; Miller & Halpern 1998). Landscape heterogeneity will probably decrease near the forest line because of increased seed availability and less stressful environmental conditions. Whereas, we expect heterogeneity will increase beyond the forest line because of distance- and elevation-induced seed dispersal decay combined with a tendency for opportunistic establishment in an increasingly unfavorable environment. We also expect favorable locales to exist throughout the abiotic setting (e.g. slope aspect, slope angle, moisture potential, snow potential, and erosion potential), and these will be important in structuring establishment patterns with increasing upslope distance from the forest line.

Materials and Methods

Study area

Mount Rainier (4392 m) is a well-known volcano and the sister mountain to Mount Fuji in Japan.

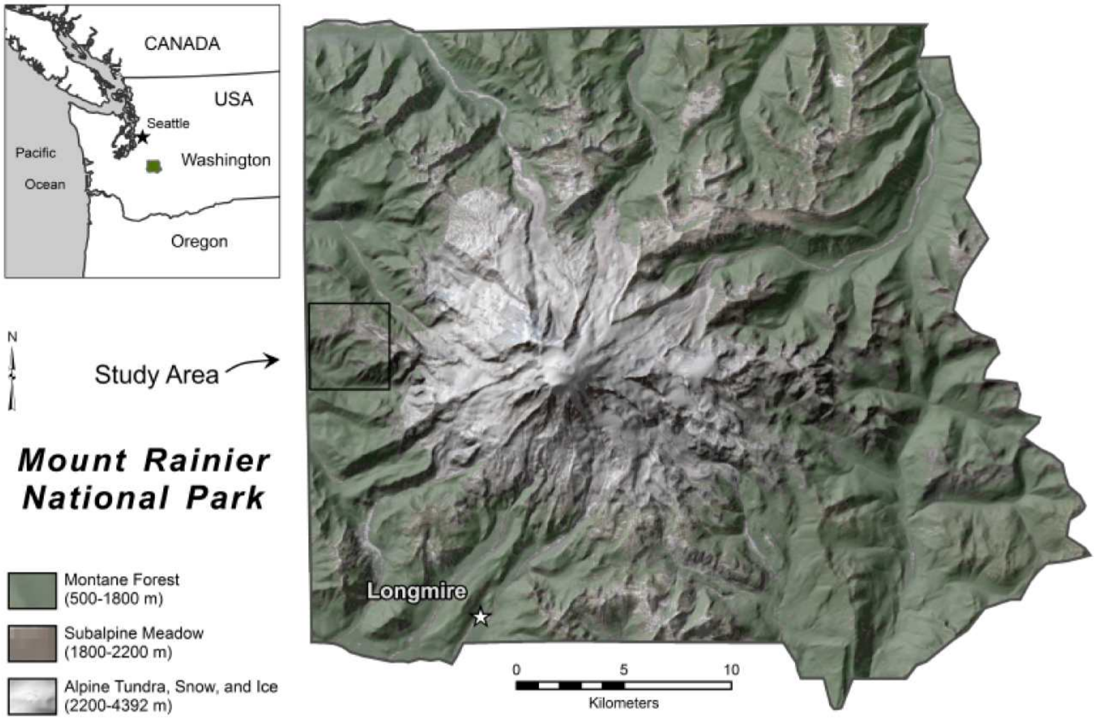

Fig. 1. The study area as denoted by modified September 2000 Landsat ETM+ imagery and a shaded 10-m DEM.

The volcano is nearly symmetrical and is located in the Cascade Range in Washington State, USA (Fig. 1). Deep valleys and many steep ridges consisting of andesite scoured by Pleistocene and early Holocene glaciers dominate the landscape. Along with glacial drift (Crandell 1969), this has created complex topographic features with widely varying microclimates that often influence patterns of treelines (Rochefort & Peterson 1996). Climate in the region can be characterized as humid temperate, with the majority of seasonal precipitation falling as snow or rain during cool winters (Bailey 1995). Prevailing southwesterly winds create a pronounced orographic effect, resulting in heavy annual snowfall of 1000-2000 cm year^{-1} on the western slopes of Mount Rainier (Hemstrom & Franklin 1982; Bailey 1995). Data from the Longmire weather station (elevation 842 m; Fig. 1) (1978-2006) indicate average monthly temperature ranged from −0.3°C in December to 16.0°C in August, average annual precipitation (rain and melted snow) was 201.4 cm, and average annual snowfall was 344.2 cm.

Snowpack may persist well into August on the western slopes, thus shortening the growing season and contributing to relatively depressed treeline elevations (~1500 m) compared to the eastern slopes (~2200 m) and other western USA treelines (Taylor 1922). The patchy structure of the subalpine parkland is thought to be primarily maintained by the depth and duration of snowpack (Henderson 1974; Franklin & Dyrness 1988). Treeline conifers include *Abies lasiocarpa*, *Chamaecyparis nootkatensis*, and *Tsuga mertensiana* that predominate on the mesic western slopes of Mount Rainier. *Pinus albicaulis* and *Picea engelmannii* are most common on the xeric eastern slopes (Rochefort & Peterson 1996). Pulses of increased establishment have been documented throughout the western half of the park during periods of warm dry summers (Franklin et al. 1971; Rochefort & Peterson 1996).

Fire is the predominant disturbance agent in the park, having affected over 90% of existing tree stands, including some treelines (Hemstrom & Franklin 1982). A 1930 fire severely burned extensive areas of high-elevation forest and subalpine parkland (1500-1800 m) near the North Puyallup River, effectively lowering the existing treeline (Hemstrom & Franklin 1982). The aerial extent of the study area is defined by the northeast Mount Wow DOQQ, which was broadly impacted by the

1930 fire. The delineated area contains approximately 150 ha of burned treeline and captures part of the steep southwest-northeast elevation gradient from the North Puyallup River (~800 m) to overarching ridges (~2000 m). The relatively xeric south and west slopes of the steepest ridges were severely burned to the krummholz (Hemstrom & Franklin 1982). Field surveillance in 2006 did not reveal any notable signs of other disturbances, such as avalanches, insect infestations, or disease.

The burned area includes numerous spurs that dissect broad south- and west-facing slopes containing complex microtopography, which can influence tree establishment patterns. *Abies lasiocarpa* is the most prevalent species near the forest line and at the upper limits of the krummholz. This species is a common invader after subalpine parkland fires, with a preference for mildly xeric sites that are topographically protected (Shearer 1984; Miller & Halpern 1998). Wind-driven seed dispersal may carry seeds up to 80 m beyond sexually mature trees (≥ 20 years old) (Noble & Ronco 1978). *Pinus albicaulis*, *Tsuga mertensiana*, and *Chamaecyparis nootkatensis* are also present, but are much less abundant.

Image preprocessing

The United States Geological Survey provided KH-4B satellite imagery from the CORONA mission 1110 for 02.06.1970. The imagery was from the aft camera and scanned at 7 µm, with a spatial resolution of ~1.9 m (McDonald 1995). We orthorectified this imagery using a parametric model and nearest neighbor resampling (Jensen 2005), in concert with direct linear transformation and bundle adjustment to build the exterior orientation (Fiore 2001). A 1.0-m United States Geological Survey color DOQQ from 21.07.2003 was used as the base aerial photography to collect ground control points (Davis & Wang 2003). We selected 42 control points that were evenly distributed throughout the 1970 imagery, with a root mean-square error of 0.495 (Jensen 2005). We used a LIDAR-based 1.8-m DEM (Terrapoint 2003) and KH-4B satellite specifications from declassified documents (McDonald 1995) to model the terrain and satellite position during orthorectification. Pre-processing procedures were employed to remove systematic errors from the DEM (Keqi et al. 2003; Rottensteiner et al. 2005) and the Minnaert correction was used to mitigate radiometric variability from the imagery, which is common in mountainous areas (Itten & Meyer 1993).

We implemented similar methods to georeference aerial photography from 1955, but we could not model the position of the airplane because of insufficient metadata. Also, clouds obscured some key areas of establishment in the photography and some locales also appeared to be pixilated. Thus, the photography was not deemed suitable for detailed mapping procedures or inclusion in the landscape metrics and statistical analyses. However, the photography did allow a qualitative assessment of tree locations before 1970.

Imagery classification, treeline identification, and change detection

We used supervised classifications tailored for high-spatial resolution panchromatic imagery to delineate trees in 1970 and 2003 (Bai et al. 2005). The green band of the DOQQ was separated for the classification analysis because the signal closely corresponds to the KH-4B panchromatic band. The green band of the DOQQ was resampled with the nearest neighbor method to match the ~1.9-m spatial resolution of the KH-4B imagery (Jensen 2005). Next, we selected 10 000 training points for each classification category representing trees, shadows (from trees), and treeless areas. We implemented a minimum distance supervised classification with a fitted modal filter to assign shadows to either trees or treeless areas, resulting in a binary classification of trees versus treeless areas.

Upper elevations (~1500 m and above) in the KH-4B imagery displayed areas of residual snowpack near some tree patches. We used 1969 aerial photography that lacked snowpack to verify whether any trees were obscured by snow, and the classification was adjusted accordingly.

The forest line was used to determine the lower boundary of the treeline and as an easily identifiable reference point for assessing treeline changes in terms of distance and elevation (Jobbagy & Jackson 2000). We visually identified and digitized the approximate position of the forest line in the 1955 imagery. Forest line in the classified 1970 satellite imagery and 2003 aerial photography was identified by using a GIS to detect the highest altitudinal limits of pixels classified as trees that were contiguously connected to closed forest. We quantified maximum and minimum forest line changes in a GIS by assessing upslope measurements from each pixel in the 1970 forest line that were perpendicular to slope contours. Treeline was defined as all pixels 30 m below the 1970 forest line and continuing to the highest elevations attained by pixels classified as trees in the 2003 aerial photography for inclusion in the landscape metrics and statistical analyses. Last, change detection was performed to identify areas of establishment at the treeline between 1970 and 2003.

Landscape metrics

The spatial complexity and variability of patch mosaics, otherwise known as landscape heterogeneity, often signify the presence of multiple underlying ecological processes (Li & Reynolds 1994). Studying the spatial arrangement of patches in relation to other abiotic and biotic variables can provide valuable insight to potentially causative ecological mechanisms involved in structuring patch mosaics (Li & Reynolds 1994). To characterize the influence of establishment on landscape heterogeneity, we used a robust landscape metric (new contagion index) and establishment rates in six different zones throughout the treeline (Li & Reynolds 1993). Elevated establishment rates combined with a more fragmented or heterogeneous landscape (i.e. low contagion value) in a particular zone indicate unique combinations of specific local site conditions that may be producing an environment more favorable for establishment.

The first zone created (A) began 30 m downslope from the 1970 forest line and proceeded 100 m upslope, closely following the curvature of the forest line. The remainder (B, C, D, E, and F) was comprised of five separate 100-m zones proceeding sequentially beyond zone A across the subalpine parkland and towards the alpine tundra. We selected 100-m zones because establishment rates beyond the 1970 forest line were sigmoidal, and each zone spanned a particular section of the sigmoidal curve. A new contagion index was calculated for each zone in the 1970 satellite imagery and 2003 aerial photography. Contagion values from 1970 were subtracted from values in 2003. Negative and positive results indicate increased and decreased landscape heterogeneity, respectively. We also determined establishment rates in each zone by dividing the number of pixels classified as trees in 2003 by the number of pixels classified as treeless in the 1970, then multiplying by 100.

Ground verification and accuracy assessment

We marked 60 ground verification points with a WAAS corrected global positioning system and used them to confirm mapped areas of establishment in the 1970 satellite imagery and 2003 aerial photography. Due to poor satellite reception, we marked 23 additional points with an uncorrected global positioning system in patches of old-growth trees. In the field, we visually identified 49 relatively stable points (i.e. 26 barren patches of rocks that did not exhibit recent signs of disturbance or vegetative growth nearby, and 23 patches of large old-growth trees). To verify the ages of young trees mapped on the imagery (i.e. 33 years or less), 15 tree ring cores and 19 cross sections were collected from widely distributed areas (Jensen 2005) within or in close proximity to mapped patches of establishment. We subjected the tree samples to standard processing before counting tree rings and determining tree ages (Fritts & Swetnam 1989). The resulting classification accuracy was 89.2% for the 1970 points and 91.6% for the 2003 points.

Local site conditions

Data for a suite of variables thought to influence establishment patterns were obtained from the processed DEM and ancillary climate data. Elevation values were extracted directly from the DEM. We calculated slope aspect and slope angle with a 3×3 window while considering all eight surrounding pixels (Burrough & McDonnell 1998). We calculated snow index values from curvature (Zevenbergen & Thorne 1987; Moore et al. 1991), southwesterly prevailing winds, elevation, slope aspect, and slope angle (Frank 1988; Burke et al. 1989; Brown 1994). Topographic concavities and leeward slope aspects at high elevations were weighted with the highest snow potential (i.e. likely to have deep season-shortening snowpack). We calculated wetness index values from the upslope catchment area and drainage patterns quantified in the DEM (Beven & Kirkby 1979; Brown 1994). Enclosed depressions with large upslope moisture catchment areas were weighted with the highest wetness potential (i.e. likely to have moist and cool soils). We determined sediment erosive index values by considering calculations of slope angle and flow accumulation from the DEM (Moore et al. 1993). Steep convex landscape features and open concavities with large upslope moisture catchment areas (e.g. ravines and stream beds) were weighted with the highest erosion potential (i.e. surfaces likely to be regularly disturbed by erosive forces). Proximity to and direction from trees existing in 1970 was calculated with standard Euclidean distance measures using the 1970 trees as source areas.

Statistical analyses

We devised a statistical approach to test the general null hypothesis that establishment patterns were not related to local site conditions. We selected binomial logistic regression for the statistical analyses because the data consisted of a nominal dependent variable with two classes and independent variables with continuous data. To assess the potential of inflated R^2 values associated with multicollinearity, we conducted Pearson correlation tests between the independent variables of 1000 randomly sampled points (Mac Nally 2000). No pairs were found to be greater than the 0.7 threshold recommended by Hosmer & Lemeshow (2000). However, we found that elevation had values above 0.6 when considered with proximity to 1970 trees and slope angle. To mitigate the effects of multicollinearity, we used *R 2.4.1* (Anon. 2006) to conduct binomial logistic regression within the hierarchical partitioning framework (Chevan & Sutherland 1991; Mac Nally 1996) and determined the relative amount of variance each independent variable contributed to establishment patterns (Mac Nally 2002). All circular independent variables (i.e. slope aspect and direction from 1970 trees) were sine-transformed to a linear format ranging from -1 (south) to 1 (north) (Zar 1999). The dependent variable was assigned 0 (treeless) and 1 (trees). Independent variables exhibited significant skewness (1.3–1.9) and kurtosis (1.1–1.7). We excluded outliers and modified the data via logarithmic and square root transformations to reduce skewness and kurtosis values below 0.5. We used a modified randomization approach with *R 2.4.1* (2006) to obtain Z-values and determine whether the contribution of each independent variable was statistically significant (Mac Nally 2002). Overall, the variance explained by each independent variable with this regression technique can be substantially lower than results acquired from traditional approaches (e.g. stepwise regression) because joint contributions from correlated independent variables and inflated R^2 values are mitigated (Mac Nally 2000).

Failure to account for spatial autocorrelation can confound statistical analyses of ecological phenomena and may result in the erroneous identification of important independent variables and their relative rankings (Griffith & Peres-Neto 2006). To address spatial autocorrelation, we used *R 2.4.1* (2006) to implement a modification of the principal coordinates of neighbour matrices approach based on eigenvectors and distance (Dray et al. 2006). We selected the Delaunay triangulation to generate the spatial weights matrix based on data-driven Akaike information criterion rankings. Results consisted of positive (i.e. similar neighbors clustered in space) and negative (i.e. dissimilar neighbors) eigenvalues in continuous data formats that corresponded well with the traditional Moran's I measure of spatial autocorrelation. We included these data as an additional independent variable in the regression analyses (Griffith & Peres-Neto 2006).

We repeated the method for each zone (A-F) discussed with the landscape metrics to gauge whether the abiotic setting becomes more important in structuring establishment patterns with increased upslope distance from the forest line. Two hundred and fifty points were randomly sampled from each zone and subjected to additional tests. After a preliminary analysis, we combined the two zones closest to the forest line (A and B) and the two zones furthest away from the forest line (E and F) because they gave similar results.

Results

Forest line changes, landscape heterogeneity, and establishment rates

The 1970 forest line was clearly higher than the approximated elevation of the 1955 forest line, but quantifying establishment rates between these dates was not possible due to the qualitative methods involved in assessing the 1955 imagery (Fig. 2). The average elevation of the forest line in the 1970 imagery was approximately 1343 m, with a minimum of 1280 m and a maximum of 1475 m (Fig. 2). The forest line had ascended upslope by 2003 to an average elevation of approximately 1453 m, with a minimum of 1400 m and a maximum of 1527 m. The smallest altitudinal forest line change between 1970 and 2003 was 0.0 m and the largest was 152 m. The smallest distance of forest line change was also 0.0 m and the largest was 264 m. We observed the majority of establishment near the lowest forest line elevation of 1280 m in the 1970 imagery and the least near the uppermost forest line elevation of 1475 m in the 1970 imagery, with the notable exception of a bare patch between 1300 and 1400 m.

We conducted the following analyses in six zones placed throughout the previously defined treeline area. Contagion difference values were 39% for zone A (Fig. 3); these decreased in zones B (– 36%), C (– 45%), and D (– 63%) before rebounding slightly in zones E (– 62%) and F (– 42%) (Fig. 3). The highest establishment rates occurred in zone A (88%) and steadily decreased in zones B (69%), C (49%), D (42%), E (27%). and F (12%) (Fig. 4).

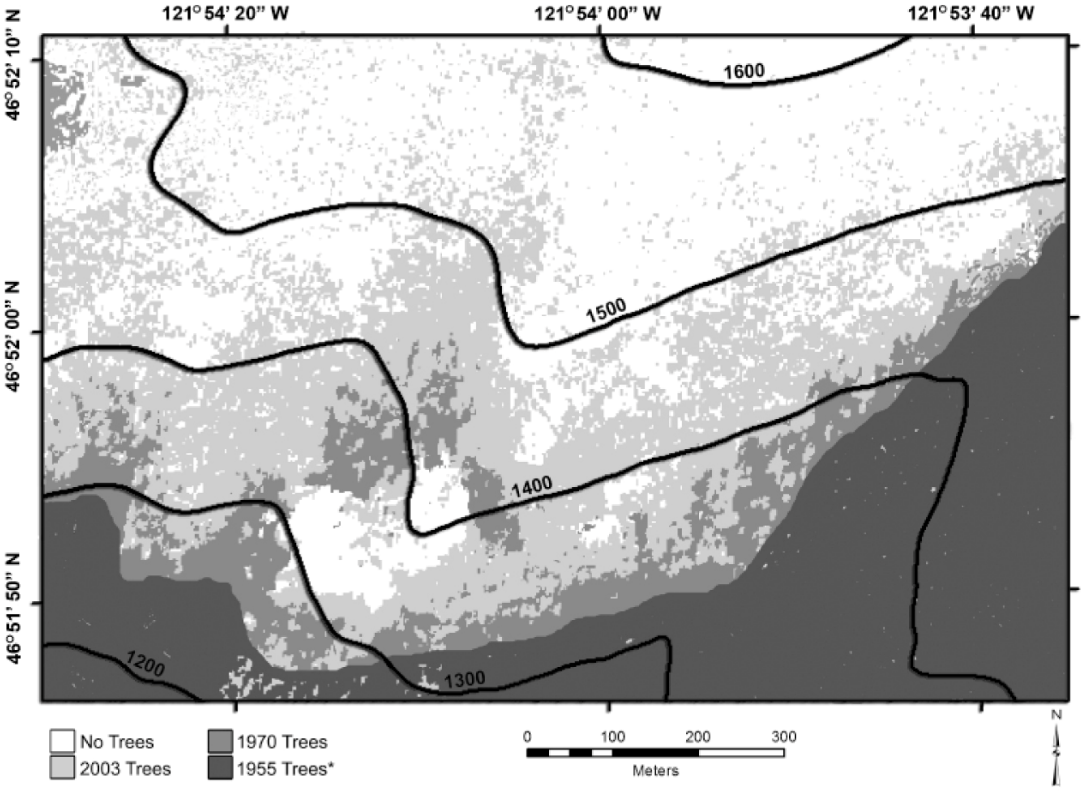

Fig. 2. Landscape patterns of tree establishment at the study site based off digitized 1955 aerial photography and classification analysis of 1970 CORONA satellite imagery and 2003 aerial photography. Dark gray denotes the approximate location of the forest line and contiguously connected trees in 1955. Medium gray represents trees present in 1970. Light gray represents trees that were newly established after 1970 and prior to 2003. The 1970 forest line follows the northern fringe of continuously connected forest depicted by the medium gray pixels. The 2003 forest line follows the northern fringe of continuously connected forest depicted by the light gray pixels. * indicates an approximation based on observations in a GIS.

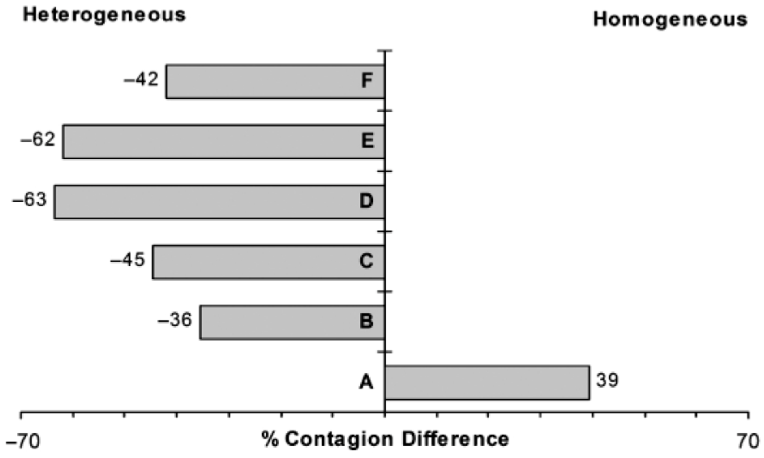

Fig. 3. Contagion differences measuring landscape heterogeneity changes between 1970 and 2003 for six consecutive 100-m zones. Zone A begins 30 m below the 1970 forest line and zone F is at the altitudinal limit of 2003 trees. Each zone follows the curvature of the forest line.

Local site conditions influencing patterns of establishment

We rejected the general null hypothesis and accepted the alternative hypothesis that local site conditions were related to establishment patterns. At a broad spatial scale (i.e. entire study area), we discovered that proximity to 1970 trees (14.1%) and elevation (11.6%) were the two most important local site conditions influencing landscape patterns of establishment (Fig. 5). Locales within 50 m of 1970 trees experienced the highest rates of establishment (~75%), before tapering off at a distance of 300 m (<10%) (Fig. 6a). Locales between 1250 and 1350 m experienced the highest rates of establishment (~80%), before gradually decreasing near 1650 m (~0%) (Fig. 6b). The elevation response also showed a definitive sigmoidal wave pattern.

Slope angle (1.9%) and slope aspect (1.4%) were also influential in structuring landscape patterns of tree establishment (Fig. 5). Moderately steep slope angles between 40° and 60° experienced the highest rates of establishment (~75%). Establishment was less likely on slope angles <40° and >60° (<60%) (Fig. 6c). In terms of slope aspect, west-, northwest-, north-, northeast-, and east-facing slopes displayed elevated rates of establishment (>80%). Relatively exposed south-facing slope aspects experienced lower establishment rates (~40%) (Fig. 6d).

Direction from 1970 trees (0.6%), wetness index (0.6%), snow index 0.4%), and erosion index (0.3%) were also statistically significant variables that influenced tree establishment patterns (Fig. 5). Leeward and relatively shaded northwest-, north-, and northeast-facing tree patch edges showed the highest rates of establishment. Decreased rates of establishment occurred on south-facing tree patch edges. Xeric to slightly mesic locales experienced the highest rates of establishment. However, extremely wet locales experienced lower establishment rates. Locales with moderate snow potential displayed elevated rates of establishment, before tapering off near exposed windblown areas and in protected sites

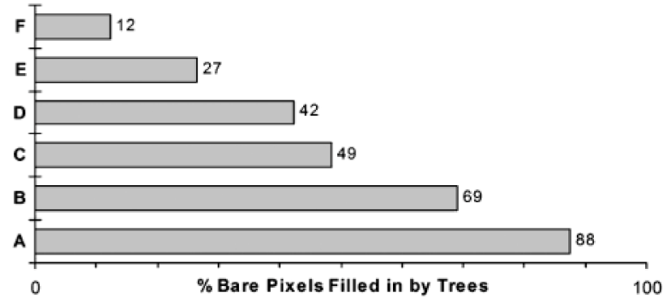

Fig. 4. Percentage of bare 1970 pixels filled by trees prior to 2003 for six consecutive 100-m zones. Zone A begins 30 m below the 1970 forest line and zone F is at the altitudinal limit of 2003 trees. Each zone follows the curvature of the forest line.

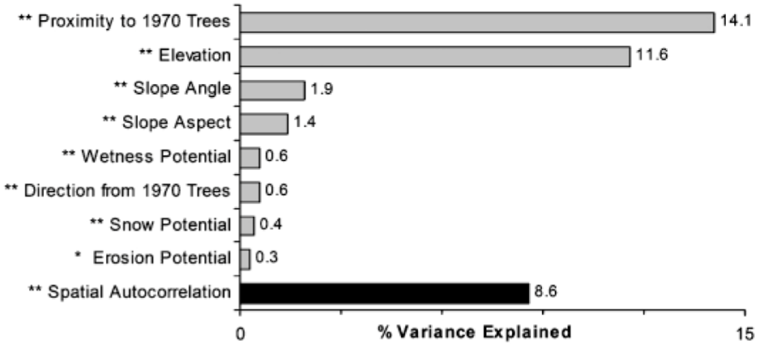

Fig. 5. Percentage of post-1970 tree establishment variance explained by local site conditions within a defined treeline area from 30 m below the 1970 forest line to the altitudinal limit of 2003 trees. Results are based on binomial logistic regressions employed in the hierarchical partitioning framework when considering the entire study area. ** indicates the independent variable is significant at the 99% confidence level, and * indicates significance at 95%.

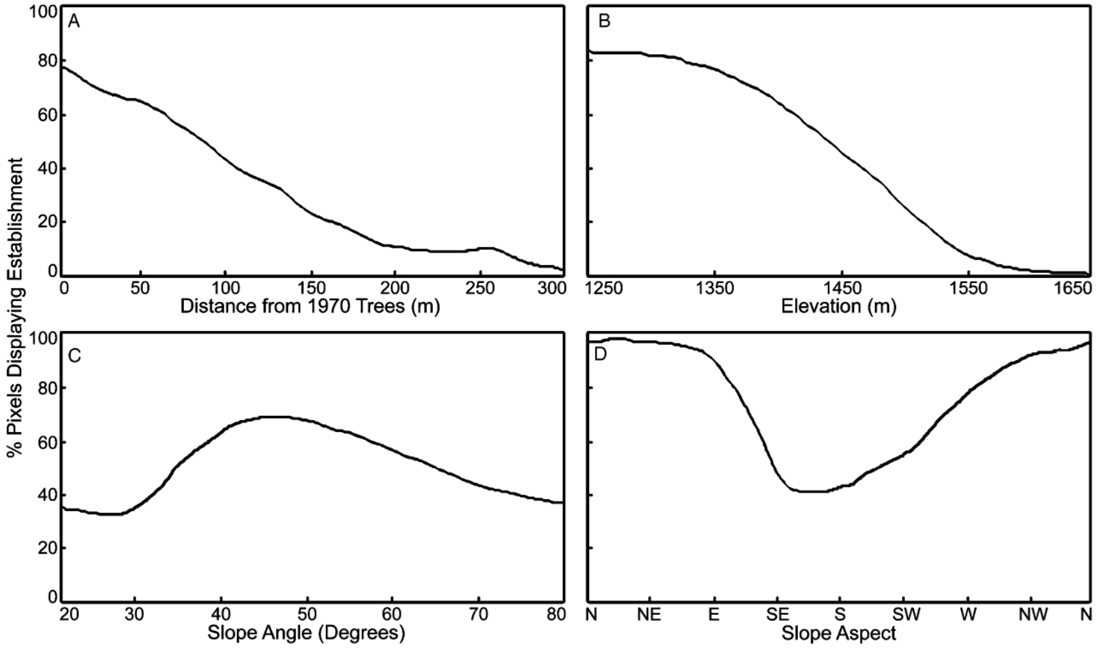

Fig. 6. Relationships between the four most significant local site conditions and post-1970 tree establishment patterns based on a defined treeline area from 30 m below the 1970 forest line to the altitudinal limit of trees in the 2003 imagery. Values were calculated from 10 000 points used in a stratified sampling scheme in order to reduce spatial autocorrelation. Fractions of pixels experiencing tree establishment were calculated at 50-pixel intervals for each independent variable (i.e. number of pixels classified as trees in the 2003 imagery divided by 50), converted to a percentage, plotted, and connected in a smoothed line graph.

with high snow potential. Locales prone to erosion displayed slightly decreased establishment rates compared to protected locales. Individually, none of these local site conditions explained >2% of the potential variance at a broad spatial scale. However, they became more important, along with slope aspect and slope angle, when examined at restricted spatial scales.

When considering the local site conditions in each of the six zones, we observed elevated establishment rates at locales similar to those reported in the three preceding paragraphs. However, there were palpable differences in the statistically ranked order of local site conditions. The two zones nearest the 1970 forest line (A and B) became nearly fully occupied by new trees and thus exhibited suppressed signals. However, we observed results in zone C nearly matching those of the entire study area, except for a peak in the importance of slope aspect (Figs 5 and 7). Several abiotic factors emerged as very important predictors of establishment with increased upslope distance from the previous zone. Slope aspect (13.1%) was the most important variable in zone D. Slope angle (5.7%) and other abiotic variables also became more important; however, proximity to 1970 trees (11.3%) and elevation (5.8%) remained important predictors in zone D. In zones E and F, the cumulative explanatory power of the local site conditions decreased slightly, with slope aspect (8.5%) and proximity (6.5%) to 1970 trees being the most important.

Discussion

Broad establishment trends

Favorable climatic conditions (i.e. warm and dry summers) probably triggered widespread establishment between 1955 and 2003. Initially, the abiotic setting appeared to play only a minor role in structuring establishment patterns. The majority of establishment occurred near existing trees and at low elevations, regardless of topographic variability; accounting for decreased landscape heterogeneity in zone A and upslope advancement of the forest line. Previous researchers have documented similar es-

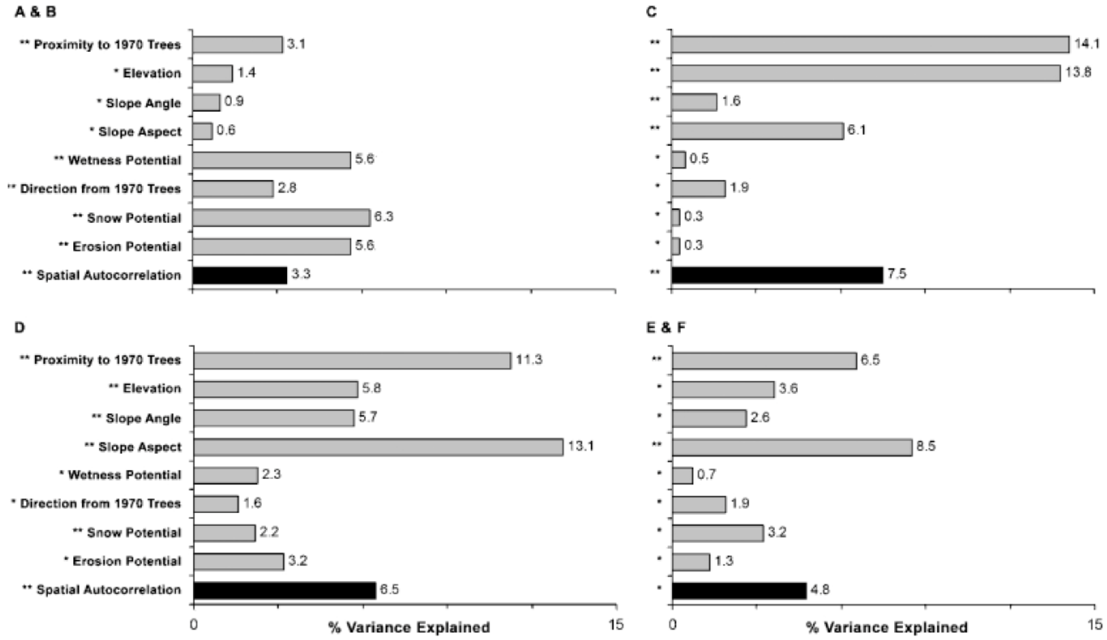

Fig. 7. Percentage of post-1970 tree establishment variance explained by local site conditions in six zones within a defined treeline area from 30 m below the 1970 forest line to the altitudinal limit of 2003 trees. Distances upslope from the 1970 forest line include 0-200 m (zones A and B), 200-300 m (zone C), 300-400 m (zone D), and 400-600 m (zones E and F). Results are based on binomial logistic regressions employed in the hierarchical partitioning framework. ** indicates the independent variable is significant at the 99% confidence level, and * indicates significance at 95%.

tablishment patterns after fire disturbance (e.g. Peet 1981; Agee & Smith 1984; Shankman 1984).

We attribute high establishment rates at these locales mostly to increased seed availability from nearby and upslope trees, but also partly to less stressful environmental conditions at low elevations (Agee & Smith 1984; Shankman & Daly 1988; Holtmeier 2003). It is difficult, however, to ignore the possibility that positive feedback mechanisms may be enhancing establishment rates at this site. Contemporary research conducted on positive feedback at the alpine tundra ecotone (e.g. Alftine & Malanson 2004; Bekker 2005; Resler 2006) suggests that it may play a critical role in structuring observed establishment patterns. Mature trees ameliorate the microclimate by increasing soil moisture-holding capacity, moderating soil temperatures, improving nutrient conditions, lengthening the growing season, and protecting seedlings from wind (Little et al. 1994; Weisberg & Baker 1995); thus initiating landscape-scale positive feedback changes into nearby exposed areas (Resler et al. 2005; Cerney 2006; Resler 2006). These assertions are consistent with the literature, which suggests establishment is highest adjacent to clusters of existing trees, before declining with distance in treeline environments (e.g. Peet 1981; Shankman 1984).

Changing roles of abiotic and biotic factors

Landscape heterogeneity was probably enhanced by reduced tree establishment rates with increases in upslope distance from the forest line (zones B-F). Heterogeneous establishment patterns throughout these zones suggest establishment became more opportunistic and that different local site conditions may be more important at restricted spatial scales. Indeed, the abiotic setting appeared to produce favorable establishment sites (e.g. protected slope aspects, moderate slope angles, moderate snow potential, moderate to low wetness potential, and low erosive potential) at high elevations beyond the forest line (zones C-F) that rivaled or became more important than proximity to existing trees and elevation (Fig. 7). These heterogeneous establishment patterns match predictions of patchy and variable establishment after fire disturbance, as dictated by a combination of slope aspect, slope angle, soil moisture, and snowpack (Shankman & Daly 1988; Noble 1993).

Potential establishment at high elevations beyond the forest line may be limited by seed dispersal decay, reduced seed viability, and approaching the physiological threshold for trees (Baig & Tranquillini 1976; Tranquillini 1979). Wind Wizard (Butler et al. 2006) suggests that the topography in the study area has a strong effect on winds, forcing the prevailing southwesterly winds, as well as westerly and northerly winds, mostly upslope, which likely carry high quantities of wind-dispersed seed (e.g. *Abies lasiocarpa)* to distant meadows. The upper threshold of seed dispersal decay is probably most limiting to establishment at the highest elevations. However, the abiotic setting appears to be crucial for facilitating establishment within the upslope seed dispersal zone at exposed locales in the harsh environment at high elevations. The sigmoid pattern of establishment we observed with elevation supports this assertion because it indicates competition between patches of different vegetative functional groups and associated influences from ecological site factors are more pronounced at high elevations, thereby reducing establishment rates (Cairns & Waldron 2003).

High rates of establishment on west-, northwest-, north-, northeast-, and east-facing slope aspects can probably be attributed to the existence of narrow diurnal to nocturnal temperature ranges, which produce fewer tree seedling fatalities when compared to relatively exposed south-facing slope aspects that are often subjected to high and low temperature extremes (Germino et al. 2002). Increased rates of establishment evident on moderate slope angles may be higher because soil is more developed than at steep slope angles and is less susceptible to geomorphic disturbances (Holtmeier 2003). Decreased establishment rates observed on shallow slope angles probably occur because existing herbaceous cover is more likely to competitively exclude invading trees (Wardle 1985; Holtmeier 2003). Animal use may also influence vegetation patch dynamics on shallow slope angles (Vale 1987; Veblen et al. 2000). These findings are consistent with the topographic preferences of *Abies lasiocarpa.*

Conclusions

This disturbed treeline in this site seems to have entered a phase of rapid establishment, triggered primarily by favorable climatic conditions. If the climate remains favorable, we expect increased seed availability to continue driving widespread establishment near the forest line and near the sexually mature trees. Positive feedback may also be a significant contributor, but our analysis offers mostly circumstantial evidence for this assertion. Reduced rates of opportunistic establishment will likely persist in favorable locales throughout the abiotic setting with increased upslope distance from the forest line. These *eco-incursions* will probably facilitate the ability of trees to become established and reproduce in the distant tundra; thereby accelerating tree invasions into exposed locales. The concerted effect of these processes will probably cause the treeline to ascend upslope. However, the width of the ecotone may become narrower in the future due to enhanced establishment rates near the forest line. Severely burned areas with few or no surviving trees near the former upper tree limit, on the other hand, may require several additional decades to recover.

It is clear that several abiotic and biotic processes are operating at different spatial scales in this study area. Vegetation scientists have long recognized that plot-scale studies may be susceptible to spatially aggregated processes, but our results indicate this phenomenon may be particularly pronounced at the treeline. Remote sensing, GIS, and spatial statistics should serve a more important role in determining suitable locations of field plots or transects. For example, vegetation scientists could use these tools to identify sites inhibiting establishment in the abiotic setting (e.g. exposed slope aspects with low snow potential) and corresponding plots could be set up to determine if microsite conditions are facilitating limited quantities of establishment in such areas.

Finally, we recognize that parts of the observed establishment patterns remain unexplained. Other variables, such as geologic substrate, edaphic properties, and independent responses of species, could modify the establishment patterns. Remnants of burned boles may also contribute to unique patterns of establishment (Little et al. 1994). These variables were either not available at a spatial grain fine enough for inclusion in this study or were indistinguishable on the photography. Future research may include (1) the use of specialized remote sensing platforms to quantify the electrical conductivity of soils and provide additional detailed edaphic information at the landscape scale, (2) plot-scale studies investigating the influences of microsites (e.g. burned boles) and species-specific responses on establishment patterns, and (3) plot-scale studies directly testing the potential influence from positive feedback. Important questions remain as to how the rankings of local site conditions tested here differ at other treelines. We suspect that the rankings are susceptible to change, particularly under different climate regimes and at other types of treeline.

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