Alpine Treeline Ecotones in the Western United States: A Multi-Scale Comparative Analysis of Environmental Factors Influencing Pattern-Process Relations

Daniel J. Weiss

A dissertation submitted to the faculty of the University of North Carolina in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Geography.

Chapel Hill
2009

Approved by,
Dr. Stephen J. Walsh
Dr. George P. Malanson
Dr. Aaron Moody
Dr. Conghe Song,
Dr. Martin W. Doyle

Abstract

Alpine Treeline Ecotones (ATE) are produced and maintained by a delicate balance of biotic and abiotic controls that function across a range of space-time scales. At regional to global scales climatic conditions are the primary controls acting upon alpine treeline. Conversely, at fine spatial scales ATE characteristics respond to localized topographic conditions that effectively mediate climatic gradients. The net result is a set of scale-dependent and geographically variable pattern-process relationships that ultimately affect morphological, ecological, and geographical characteristics of the ecotone. Previous ATE research has rarely examined the role that scale and space play in the complex relationships between environmental conditions and the ATE. The research presented in this dissertation furthers the understanding of ATE dynamics by examining how relationships between ATE features and abiotic controls vary across space and with scale through an analysis that includes multiple ATE study sites distributed throughout the US American West. Furthermore, this research develops innovative methods for measurement, characterization, statistical analysis, and modeling of the ATE using geo-spatial data sources including satellite imagery and digital elevation models.

Preface

This dissertation represents years of work and thought that were made possible thanks to the generosity, patience, assistance, and sacrifice of so many people. First and foremost, I am indebted to my wife Ardys for being a constant source of strength during what was all too often an arduous journey. The support she provided so unselfishly, despite all the lonely nights I spent working in the lab and the months I spent in the field, is a testament to the boundless patience, kindness, and love that she possesses. I am also grateful for the love and support provided by parents. Although we didn't see each other often enough during my time in Carolina, knowing they took pride in my success buoyed me through many moments of self-doubt.

From a professional standpoint, I am profoundly thankful for the support and guidance provided by my advisor Steve Walsh. I'd be hard pressed to describe all the things I've learned from Steve over the years, but I am undoubtedly more skilled technically, more grounded theoretically, and more polished and prepared professionally thanks to Steve. I'll always admire how he knew when to provide guidance and when to give me the freedom to find my own path. Should I advise students of my own in the future, I will have a tough act to follow.

I also acknowledge the important role played by my committee in shaping the work within this dissertation. George Malanson, Aaron Moody, Conghe Song, and Martin Doyle were generous with their time and have influenced my work through direct input, classroom instruction, and time in the field. I sincerely appreciate their effort on my behalf, and my work is substantially better for it.

Several institutions provided funding for my research including USGS (i.e., a Western Mountain Initiative grant), the UNC Graduate School (i.e., a dissertation completion fellowship), and the UNC Geography Department (i.e., travel support for fieldwork, three semesters as a teaching fellow, and one semester as a TA). Without these funding sources my work would not have been possible and I am appreciative for the support these institutions provided.

Finally, I would like to acknowledge the members of the UNC Geography Department, and especially those in the spatial analysis lab, for helping me through countless challenges over the years. The benefits of working with and around such bright and considerate people were obvious whenever the answer to a question was at the ready or a favor was needed. On a more personal note, I enjoyed my time in Chapel Hill tremendously, and I feel lucky that there were very few distinctions between colleagues and friends within the department. I genuinely enjoyed coming to the office, even on days filled with tedious processing, because such wonderful people surrounded me. Many people deserve mention, but I would most like to acknowledge Tom Whitmore, Yang Shao, and Evan Hammer for their friendship and support.

TABLE OF CONTENTS

LIST OF TABLES

Table

LIST OF FIGURES

Figure

LIST OF EQUATIONS

Equation

CHAPTER 1

DISSERTATION OVERVIEW

1.1.0 Introduction

The alpine treeline ecotone (ATE) is defined as the transition zone between the closed-canopy subalpine forest and the highest individual trees or tree patches found upslope (e.g., Holtmeier 2003). Typical landcover in the ATE includes upright trees growing as individuals or in small patches, krummholz (i.e., climatically stunted and shaped) trees and tree patches, alpine meadows, alpine tundra, semi-permanent snow and ice, and bare soil or rock. The alpine treeline ecotone is spatially and compositionally complex, and may exhibit dramatic changes in organizational pattern and/or structure over short distances. Much of the variability within the ATE can be attributed to abiotic variables because they influence vegetation patterns, landscape composition, and the position of the ecotone (Walsh et al. 2003).

The ATE is an area of ecological research interest for many reasons, most notably for the identification of landscape responses to global climate change and for the construction of predictions about future ecological dynamics. The critical scientific questions associated with climate change and its affects on the ATE include the identification of areas where changes are likely to occur, the changes that can be expected, and the magnitude and speed of such changes. Furthermore, the ATE merits scientific attention and study because of its ecological sensitivity; its status as a boundary-layer between distinctly different eco-types (e.g., forests and tundra) that fulfill unique ecological functions; and the ecosystem goods and services that are influenced by the ecotone such as biodiversity, carbon and nutrient fluxes, and their cascading effects to other ecological systems (Körner 2003). The broader societal significance of the ATE includes its relationship with mountain snowpacks, a major water resource in many arid and semi-arid regions; its function as habitat for numerous iconic and/or threatened species, such as the grizzly bear; and the economic value of the amenity resources of alpine settings to the tourism industry and individual well-being.

ATE researchers have long sought to explain how environmental processes produce the characteristic patterns and features of the ecotone (Holtmeier 2003). This research has generally been conducted at two distinctly different scales: regional to global (i.e., coarse) and individual trees to the hillslope (i.e., fine); with comparatively little research focused on intermediate scales of analysis. Previous research on the ATE conducted at coarse spatial scales has consistently found treeline position to be highly correlated with climatic gradients (e.g., Körner 1998b). In contrast, ATE research at finer spatial scales typically relates ATE heterogeneity to a complex set of interacting environmental variables and conditions, including topographic characteristics (e.g., Bunn et al. 2005b, Hofgaard and Wilmann 2002, Rupp et al. 2001), disturbance regimes (e.g., Walsh et al. 1994), geomorphic effects (e.g., Butler et al. 2004, Resler 2006), and feedback processes (e.g., Alftine and Malanson 2004, Bekker 2005, Malanson 1997). Important aspects of ATE controls that are less well understood include: (1) how the hypothesized environmental controls vary at intermediate scales, thereby linking local processes to regional or global patterns; (2) how hypothesized ATE controls vary with space over a geographically diverse set of conditions, and (3) how ATE vegetation patterns relate to underlying environmental controls, when both ATE vegetation and hypothesized environmental controls are geographically contingent.

The research presented in this dissertation addresses gaps in the existing ATE literature by analyzing the effects of spatial scale and geographic location on relationships between hypothesized ATE controls and treeline characteristics including elevation, tree presence and absence, and pattern, for study sites distributed throughout the western United States. This research differs from previous work by (1) collecting detailed micro-site measurements of ATE characteristics across a diverse, regionally distributed set of study sites; (2) associating a consistent set of environmental variables with each ATE sample by applying uniform sampling techniques to comparable data sources; and (3) analyzing the data using frameworks that facilitate ATE characterizations at multiple spatial scales, thereby allowing within- and between-site comparisons that assess the form and pattern of the ATE. The need for such studies was identified by Holtmeier (2003, p. 21) who stated "a better understanding of the ecological situation and the spatial and temporal dynamics in the ecotone requires extensive local and regional studies on microsite conditions and microsite patterns specific to the ecotone…"

1.2.0 Background - Ecotones

The term ecotone was coined by Clements (1907, as cited in Harris 1988) and was initially defined as a region of stress between adjacent ecological communities. While the term ecotone has since been used in many different contexts, the original usage of the term is still relevant for this research, as alpine treelines separate the subalpine forest community from communities found upslope above, such as alpine tundra. Ecotones are produced by species and individual responses to abiotic conditions (i.e., thresholds that exceed the physiological limitations of flora and/or fauna), as well as biotic interactions between species and individuals that are manifested though competition and facilitation (Gosz 1992). Furthermore, biotic processes are, in some cases, able to modify abiotic conditions, thereby improving and/or degrading habitat for one or more species found within ecotones. These biotic processes may produce non-linear relationships (e.g., ecotones may not move gradually, but in relatively rapid shifts if micro-habitats are changed following the establishment of pioneer individuals) typified by feedback processes (Wilson and Agnew 1992). For example, Weins et al. (1985) theorized that edaphic conditions, produced partially though biotic processes, are fundamentally responsible for patterns visible at ecotones.

Due to the varied interpretations of what, exactly, constitutes an ecotone, attempts have been made to clarify and standardize the term. Leading these efforts are review papers intended to make research more comparable across sites and conditions, thereby encouraging theoretical advancements in the understanding of ecotones. One such paper was provided by Gosz (1993), who created a classification system that defines ecotones by the spatial scale of analyses used to examine them. Scale was selected as the defining characteristic because it is a fundamental factor for indentifying the specific process(es) producing and maintaining ecotones (e.g., preventing ecotone migration or maintaining existing patterns). This ecotone classification system consists of biome, landscape, patch, population, and plant ecotones, with the first three being controlled primarily by abiotic factors (e.g., climate, topography, and soils) and the final two being controlled primarily by biotic processes (e.g., competition and physiological properties of plants). More recently Strayer et al. (2003) explored the general term "boundary," as used in ecology, and identified four methodologies commonly employed for classifying and characterizing boundaries. These authors found that ecotones are typically defined according to their (1) origin and maintenance, (2) spatial structure, (3) boundary function, or (4) temporal dynamics. Furthermore, these authors suggest that more specificity is required when describing ecological boundaries due to the diversity of boundary types in existence.

There is a rich history of research exploring the causes and effects of naturally occurring ecotones. Risser et al. (1995) provides an informative discussion of historical ecotone studies and current research (as of 1995) on this subject. Important topics addressed by these authors include the (1) relationship between ecotones and biodiversity (i.e., they are typically species rich compared to adjacent biomes) (e.g., Delcourt and Delcourt 1992, Leopold 1933); (2) the influence of ecotones on flows of resources such as nutrients and water (e.g., Baron et al. 1994); (3) ecotones as habitat (e.g., Lidicker 1999); and (4) the association of ecotones with global change (e.g., Noble 1993). Furthermore, the nature of studies that associate ecotone responses to global change tend to take advantage of common ecotone properties such as the dominance of water balance (e.g., Allen and Breshears 1998) and temperature (e.g., Arris and Eagleson 1989) as controls at the biome level, and species-environment interactions acting as key controls at local levels (Ries et al. 2004). Exploring ecotones within the context of limiting resources has great utility because ecotones may contain species existing at the limits of their environmental tolerances that stand to be greatly affected by changing conditions (Baron et al. 2000). Specific ecotone responses to changing conditions will depend on the rate and magnitude of change (Kullman 1995, Macdonald et al. 1993), tolerances of individual species (Breshears et al. 2005), interspecific competitive and/or facilitative relationships (Baumeister and Callaway 2006, Callaway 1998, Lingua et al. 2008, Walker et al. 2003), species' dispersal abilities (Peters 2002, Weltzin and McPherson 1999), and threshold responses of species (Gosz 1992). Also of interest are new limitations that may arise in areas where they did not previously exist, such as moisture stress in areas now experiencing warmer temperatures, and changes in the magnitude, type, and/or frequency of disturbances (Neilson 1993). New limitations are also likely to affect existing competitive and/or facilitative relationships among species (Batllori et al. 2009).

1.2.1 Background - ATE

ATE patterns and processes have been attributed to numerous environmental conditions, the foremost of which are abiotic factors expressed as biophysical gradients (Stevens and Fox 1991). Due to the practical challenges of sampling a very heterogeneous, globally distributed ecotone, existing ATE analyses conducted at coarse spatial scales have focused on simple statistical relationships between ATE elevation and environmental variables. Results from such coarse scale ATE analyses have consistently associated elevation with temperature, although the specific temperature metric has varied (Körner 2003). For instance, Körner (1998b) found the strongest relationship between treeline elevation and mean growing-season air temperatures between 5.0 and 7.5 degrees Celsius for alpine treelines outside of the tropics. Controls on the ATE, however, are more complex than a simple temperature boundary, because at fine spatial scales numerous environmental factors affect ATE characteristics directly or indirectly by effectively mitigating or enhancing macro-scale climatic controls (Seastedt et al. 2004).

ATE research conducted at fine spatial scales may produce simple statistical relationships similar to those from coarse scale ATE studies. However, results from fine scale ATE research vary widely with geography and cannot be easily attributed to a single variable such as air temperature. For example, conditions important for ATE vegetation at fine spatial scales may include geomorphic controls (Butler et al. 2003), microtopographic effects (Resler et al. 2005), sky exposure (Smith et al. 2003), soil temperature (Körner 1998a), herbivory (Cairns and Moen 2004), soil fertility (Malanson et al. 2002), and soil moisture (Bunn et al. 2005a). Another challenge for assessing the geographic variability in ATE controls at fine spatial scales is making comparisons between study sites that necessitate different sampling and analytical approaches to explore.

Despite a multitude of possible fine scale ATE controls, many of which may simultaneously affect single sites, ATE research findings were effectively reduced into a simple typology by Holtmeier (2003). This typology essentially distills the universe of complex and geographically variable examples of the ATE into two general types of timberlines: climatically- and orographically-controlled. This simple typology associates treeline pattern-process relations with the dominant environmental control(s) acting upon the ecotone. Within this framework, climatic treelines are limited primarily by air and/or soil temperatures, and/or precipitation. In contrast, orographic treelines are limited by steep and/or unstable slopes that are not conducive to soil development and/or tree establishment. Treelines influenced by disturbances form a third category with which to define the ecotone. However, Holtmeier (2003) defined disturbed treelines as orographically-controlled because snow avalanches and forest fires, the most prominent disturbance types for mid- to high-latitude alpine treelines, are affected by topographic conditions.

More in-depth ATE analyses conducted at the scale of the individual tree focus on identifying the mechanisms affecting (1) tree mortality, (2) increases in size, or (3) seedling establishment in treeless areas within or just above the ecotone. Körner (2003) summarized these mechanisms into five basic hypotheses of treeline formation that are: (1) frost damage, (2) winter desiccation, (3) reproduction limitations, (4) carbon balance, and (5) resource utilization. Frost damage has largely been dismissed as a major control on ATE trees because plant species living in the ATE are well adapted to the local environment and can survive long and cold winters. Growing season frosts, however, are significant and may contribute to stunted growth forms. Winter desiccation (i.e., frost drought) occurs when conifer needles are exposed to blowing snow and ice, and intense solar radiation (i.e., direct and reflected), as they project through snow that covers them during the winter months.

Tranquillini (1979) believed desiccation to be a major control on ATE areas outside the tropics because it prevents trees from (1) establishing without some sort of micro-topographic shelter and (2) growing taller than the depth of snow that accumulates in the sheltered areas. Reproductive limitations pertain to seed supply, seed dispersal, and seedling establishment for ATE tree species. In ATE areas, trees commonly produce few viable seeds, but seed supply is seldom a constraint on the ATE as trees in adjacent subalpine forests do not suffer from such harsh conditions and typically produce ample seed as a result. Dispersal plays an important role with respect to treeline pattern and position (Malanson and Cairns 1997), but it is a less critical limitation in the ATE than in other ecotones because of the relatively short distances that seeds must travel to reach the ATE from nearby source areas. Limitations to seedling establishment are important with respect to the ATE because treeline movement and/or infilling between tree patches occurs only if seedlings can establish in previously uncolonized sites (Smith et al. 2003). The carbon balance hypothesis suggests that trees in ATE areas are limited because their respiration demands exceed their gross primary productivity, due to factors such as low air and/or soil temperatures and, possibly, low partial pressure of carbon dioxide. This hypothesis has not been widely supported with empirical evidence, as trees within the ATE seem to photosynthesize sufficiently to meet their respiration demands (Körner 2003). Cairns and Malanson (1998) report, however, that the carbon balance hypothesis has some utility for explaining vegetation characteristics within the ATE through a biogeochemical model that includes winter injury as an additional limitation. Resource utilization hypotheses are based on the idea that trees in the ATE are sufficiently productive to offset respiration demands, but transfers of resources within the trees are hampered by environmental conditions, in particular low temperatures. With the exception of work focused on seedling establishment (e.g., Germino et al. 2002), a significant drawback to the research summarized by Körner (2003) is that it focuses primarily on the health of established trees and has yet to be applied to seedlings, for which limitations may be very different (Smith et al. 2003).

Within the context of multiple hypothesized causes of alpine treeline and their associated abiotic and biotic controls, a challenge has been to extend understanding of the environmental controls affecting the ATE across spatial scales that range from the individual plant, to the landscape, and eventually to the region. Unlike ATE research conducted at coarse and fine scales, examinations of environmental variables hypothesized to affect the ATE at intermediate scales have primarily been limited to theoretical frameworks. Unfortunately, due to the challenges of conducting detailed analyses that incorporate widely dispersed study sites, these theoretical frameworks generally lack associated empirical tests with which to validate pattern-process relationships relevant for scales between the hillslope and the region. Three noteworthy theoretical frameworks that incorporate intermediate ATE controls were conducted by Billings (1979), Seastedt et al. (2004), and Holtmeier and

Broll (2005), each of which was designed to incorporate the scale-dependent relationships between ATE controls and characteristics. Billings' (1979) research divides ATE controlling factors into three categories: macro-gradients, meso-topographic (based largely on Billings (1973)), and micro-topographic. According to this framework, ATE patterns are produced through a combination of bedrock influences and meso- and micro-topographic effects, with biotic interactions contributing by softening abiotic controls. Seasted et al. (2004) added to the work by Billings (1979) by including soil properties and nutrient fluxes into the meso-topographical conceptual model. Holtmeier and Broll (2005) incorporated biotic and abiotic controls and disturbances across a range of spatial scales into a conceptual model of ATE controls. The model presented by Holtmeier and Broll (2005) is the most ambitious in the sense that it ascribes an approximate spatial scale of influence to many hypothesized ATE controls.

Research that explores ATE patterns and processes at intermediate spatial scales generally compares study sites that, while not regionally distributed, extend beyond the hillslope. An example of such a study was conducted in northern Patagonia by Daniels and Veblen (2003). These authors used a combination of field sampling and air-photo interpretation to compare climatic and disturbance related ATE controls on eastern and western slopes of the Andes. More commonly, ATE pattern-process studies have focused on finer spatial scales, such as National Parks in the western United States. Such projects frequently cover sufficiently large geographic areas to incorporate analyses that utilize remotely-sensed imagery and GIS data. These digital datasets are useful for characterizing site conditions, vegetation states, treeline components, lithologic types, and disturbance regimes, in a spatially-explicit way. Digital datasets may also be applied to studies that examine ATE sites over time through air-photo or satellite image time-series. Examples of ATE research in National Parks include studies by Brown (1992, 1994a, 1994b), Brown et al. (1994), Allen (1995), Allen and Walsh (1996), and Baker and Weisberg (1995). Of these, Allen (1995) and Allen and Walsh (1996) are particularly relevant to this research because they assessed environmental controls on treeline patterns. Other relevant research includes gradient analysis in alpine communities (e.g., Urban et al. 2000), scale-dependencies of alpine vegetation and topography (e.g., Bian and Walsh 1993), geomorphic controls on ATE tree patterns (e.g., Butler et al. 2003), influences of ecological feedbacks leading to changing ATE patterns (e.g., Malanson et al. 2000), and the paleoclimatic drivers of spatial and temporal patterns within the alpine treeline (Bunn 2004, Kullman 1995, Lloyd and Graumlich 1997).

The ATE has also been the focus of research examining the ramifications of global climate change, as alpine ecosystems are particularly vulnerable to such changes due to their ecological sensitivity (Kupfer and Cairns 1996). The ATE can be viewed as a potential climate change indicator as its position and form may vary in response to local, regional, and global changes. Evidence of significant shifts in the elevation of the ATE, since the end of the Pleistocene, has been found in alpine areas of the western United States (Lloyd and Graumlich

1997, Whitlock et al. 2002). Evidence of shifts in treeline elevation within the last century has been found in Scandinavia (Kullman 1996, Kullman and Oberg 2009). However, in most alpine areas an important drawback to using treeline elevation as a climate change indicator is the slow rate of ecotone movement (e.g., Butler et al. 1994) due to harsh environmental conditions (Körner 2003), geomorphic processes that constrain or encourage treeline expansion (e.g., Butler and Walsh 1994), and disturbances that can depress treeline below its ecological maxima (e.g., Walsh et al. 1994). In the absence of rapid ecotone movement, several other indicators have been proposed for assessing climate change-related responses within the ATE. These indicators include seedling invasion of alpine meadows and alpine tundra patches located within the ATE (Baker and Weisberg 1997), changes in the growth forms of trees within the ATE, changes in the productivity or growth rate of ATE tree species (Paulsen et al. 2000), and seedling establishment beyond the current elevation limit (Smith et al. 2003). Therefore, patterns within the ATE may be a more practical tool for assessing treeline responses to climate change than searching for evidence of changes in treeline elevation. Multiple environmental limitations acting upon individual treelines are also important within the context of climate change, as these controls are interrelated with respect to vegetation. As such, changes to one control may lead to new limitations, such as higher air and soil temperatures leading to water stress.

1.3.0 Theory

Hierarchy theory forms the theoretical cornerstone for this research by providing a basis for understanding how landscape patterns and characteristics are related to ecological processes across multiple spatial and temporal scales. Other useful theoretical frameworks include complexity theory, elements of niche theory, theories of plant succession, the vegetation-switch concept, and the central-place-foraging hypothesis. Although these concepts can be discussed as unique theoretical elements, they overlap significantly with respect to ATE vegetation dynamics.

Hierarchy theory is based on the ideas that (1) processes occurring within any level of a system are constrained by levels above their characteristic scale, and (2) lower level processes lead to emergent patterns and behaviors that describe levels above the characteristic scale (Allen and Starr 1982). Hierarchy theory, therefore, frames the scaling component of this research by providing a context for explaining ATE vegetation in terms of plant and patch level processes that affect landscape level patterns, as well as landscape-to-regional level constraints upon pattern-process relations. A particularly notable application of hierarchical thinking to the study of ecotones was provided by Gosz (1993).

Complexity theory (e.g., Cilliers 1998) is valuable for understanding ATE vegetation because it helps explain non-linear dynamics, including responses to threshold conditions, potential positive and negative feedbacks, self-organization, and the emergence of patterns. An example of a threshold condition within the

ATE is stem escape from krummholz vegetation patches (i.e., stems growing taller than the relatively smooth-topped upper layer of needles (Tranquillini 1979)). In this process, seemingly favorable climatic conditions may not lead to stem escape if such conditions are required for several consecutive years to exceed a system threshold. Only when such a threshold is exceeded can sufficient growth occur above the existing krummholz mat to create a new upper boundary layer of the patch capable of withstanding periodic harsh years. Positive and negative feedbacks are relevant within the ATE as they can introduce non-linear responses through modifications of micro-environmental conditions. Feedbacks may maintain, reproduce, and/or expand existing ATE patterns and conditions, or alter the trajectories of ATE features and systems (Wilson and Agnew 1992). Examples of feedbacks within the ATE include sheltering effects from existing vegetation that protect seedlings from damaging wind and sun exposure, as well as trapping blowing snow that provides winter insulation and growing season moisture.

A useful conceptual framework for linking complexity theory and hierarchy theory (and its predecessor, systems theory) is potential capacity, in which all possible states of a landscape are limited by conditions present at coarser scales (Frissell et al. 1986). Within this framework, changes in the state of a system at a given level can change patterns and behaviors that are visible in the level above the characteristic scale, but these changes cannot fundamentally alter the state of the level above. In contrast, changes in higher level states may not alter any patterns or processes in levels below the characteristic scale, but such changes can modify the potential capacity of lower levels. Within this theoretical framework, changes to higher level states can be viewed as thresholds exceeded, and the potential states of a system that are produced through self organization, can be viewed as attractors.

Landscape ecology provides a framework for exploring how heterogeneity within the abiotic environment (in this case, limiting resources within the ATE) produces scale-dependent patterns visible in the landscape (Turner 1989, Wiens et al. 1993). Landscape ecology also provides a general explanation for the production of landscape pattern through the complex interactions between abiotic conditions, biotic processes, and disturbance (Turner et al. 1991). An earlier, although related, explanation for the causes of landscape pattern was provided by Levin and Segel (1976), who suggested that patterns are a function of local uniqueness, including abiotic conditions and random chance; successional phase; and dispersal. Holtmeier (2003) effectively merged these definitions when he described vegetation character within the ATE as the complex result of species composition, successional stage, past and present conditions, and disturbance.

Elements of niche theory are also useful for understanding ATE pattern within the context of abiotic constraints. For example, Grinnell (1917) define the niche as the spatial distribution of species, as limited by their functional and structural constraints relative to the environment in which they exist. Also important for understanding ATE vegetation is the concept of interspecific competition, which is linked to Grinnell's original niche theory by Gause (1964). This linked approach provides a mechanism for explaining the disparity between the fundamental and realized niches for species or communities. Hutchinson's (1957) concept of an N-dimensional fundamental niche space, with axes composed of environmental variables, also fits well within this research. With respect to the ATE, evaluating ecological niche space depends on the species or community of interest. For example, alpine tundra may be well suited to cover all of the ATE, but tree species have a competitive advantage in favorable micro-sites where they can displace tundra species. In contrast, tree species within the ATE may be at the extreme edge of their fundamental niche, yet remain relatively unaffected by competition from tundra.

Theories of plant succession are helpful for understanding processes occurring in the ATE as (1) they help explain the biotic component of pattern formation through ecological processes, such as competition and dispersal, and (2) any movement of an ecotone may involve one vegetation type succeeding at the expense of another (although this is not always necessary as many treelines are adjacent to non-vegetated areas). The two classic views on succession are Clements' holistic view and Gleason's individualistic view. Clements' view is useful if we consider the closed-canopy subalpine forest and the alpine tundra to be distinct vegetation communities, each with emergent properties, that are in direct competition at the ATE. However, ultimately, Clements' theory is less applicable for the ATE because community changes can occur in either direction (i.e., from forest to tundra or vice versa) or not at all, depending upon the environmental conditions of the treeline. In contrast, Gleason's view can be applied to the ATE because complex landscape patterns are the result of species, patch, and individual responses to environmental constraints, including the ability to create and/or take advantage of favorable micro-site conditions. Additional support for Gleason's view of succession in alpine vegetation was provided by Whittaker (1975) who found that ranges of plant species in the Sierra Nevada were not strongly associated at the community level. Other important elements of succession theory come from Connell and Slayter (1977) who described basic succession causality including facilitation, inhibition, and tolerance. These causality types are particularly useful when seedling establishment occurs within or close to krummholz patches (i.e., facilitation) compared to establishment in tundra-covered areas (i.e., inhibition).

The concept of a vegetation switch (Wilson and Agnew 1992) explains the occurrence of ecotones in the absence of abrupt changes in environmental conditions as a result of positive feedbacks within the biotic community. This model is very applicable for the ATE, which was actually the ecotone used as the study area for Wilson and Agnew's research, because only slight changes along abiotic gradients lead to major changes in species composition for this relatively narrow ecotone (Wiegand et al. 2006).

Finally, the central-place-foraging hypothesis is useful for explaining some of the vegetation responses in the ATE. Although several hypotheses exist for why trees have stunted growth forms in the ATE, including to avoid desiccation (Tranquillini 1979) and to decouple the internal patch temperature from the air temperature (Körner 2003), the central-place-foraging hypothesis allows us to consider stunted growth forms within the context of a cost-benefit ratio. The general idea is that the resource cost of root growth required for increased height is not rewarding because cold soil temperatures limit flows of resources from the roots to the leaves or needles (Körner 2003).

1.4.0 Study Area

The study sites for this research consist of 26 alpine areas distributed throughout the western United States (Figure 1.1). All of the study sites possess mountainous terrain and alpine treeline ecotones. The sites are also distributed over a range of thousands of kilometers and exist under dramatically different environmental conditions, thereby creating an ideal, albeit challenging, laboratory for a regional scale characterization and comparison of the environmental controls influencing the ATE.

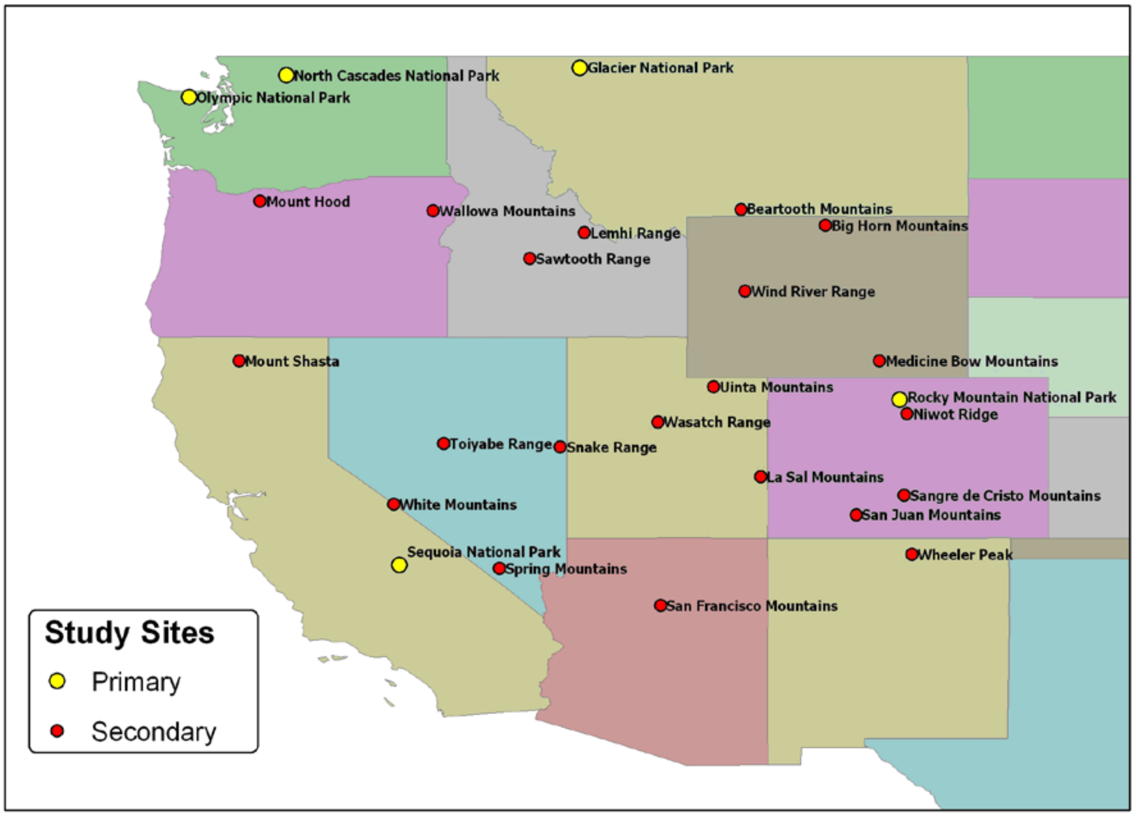


Figure 1.1: ATE study sites within the western United States.

Primary study sites include five National Parks that are a part of the Western Mountain Initiative (WMI) of the US Geological Survey and, therefore, have been the sites for extensive ATE research. These sites include Glacier National Park, Montana; Rocky Mountain National Park, Colorado; Olympic and North Cascades National Parks, Washington; and Sequoia and Kings Canyon National Parks, California. Secondary study sites for this research include Mt. Hood and the Wallowa Mountains, Oregon; Mt. Shasta and the White Mountains, California; the Toiyabe Range, the Snake Range, and the Spring Mountains, Nevada; the San Francisco Peaks, Arizona; Wheeler Peak, New Mexico; the

Wasatch, Uintas, and La Sal Mountains, Utah; the San Juan Mountains, Sangre de Cristo Mountains, and Niwot Ridge, Colorado; the Medicine Bow, Wind River, and Bighorn Ranges, Wyoming; the Beartooth Mountains, Montana; and the Lemhi and Sawtooth Ranges, Idaho. Secondary sites were selected to provide study sites in geographic settings between the primary sites, thereby facilitating the spatial analytical component of the research by allowing (1) ATE pattern-process relations to be explored beyond intra-park scales and (2) cross site comparisons. In total, the 26 study sites represent different ecological and geographical extremes of the ATE within the western United States (e.g., wet, dry, warm, and cold sites).

The regional distribution of the study sites allows this research to incorporate a wide range of environmental conditions coincident with alpine treelines, including dramatic climatic gradients, various geologic conditions, and different mountain arrangements (i.e., isolated peaks vs. expansive ranges). Major climatic gradients include (1) the north-south temperature gradient, produced primarily as a function of latitude and its effect on incident solar radiation, and (2) the west-east precipitation gradient, produced by a combination of distance from the dominant moisture source (i.e., the Pacific Ocean), orographic precipitation, and rain shadows. Geologic conditions in the study areas range from granitic rocks in the Sierra Nevada and Southern Rocky Mountains, to brittle sedimentary strata in the Northern Rocky Mountains, to basaltic rocks in the Olympic Range, and to Andisitic formations in the Southern Cascades.

Another important aspect of the regionally distributed study sites is the influence of tree and shrub species composition on ATE dynamics. According to tree species range maps (Little 1971), there are no tree species common to the ATE that are found in all 26 sites. Twenty sites, however, do possess limber pine (*Pinus flexilis*). Limber pine is identified as an important ATE species due to its role as a pioneer species that can provide micro-topographic shelter for recruitment and establishment of trees (Rebertus et al. 1991). Whitebark pine (*Pinus albicaulis*) fulfills similar roles to limber pine in the ATE (Resler 2006), but is less common throughout the region. Another commonly found species is lodgepole pine (*Pinus contorta*), which is found in 19 of the 26 study sites, and is typically associated with ATE areas that have experienced forest fires. Douglas fir (*Pseudotsuga menziesii*) is another widespread species that is much more prominent at lower elevations, but does occasionally grow in the ATE, particularly in the Northern and Central Rocky Mountains.

In general, the ATE areas in the Rocky Mountains are dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). ATE areas in the Pacific Northwest also have abundant subalpine fir, but mountain hemlock (*Tsuga mertensiana*) is more commonly found here than Engelmann spruce. Engelmann spruce, subalpine fir, and mountain hemlock are noteworthy because they may form krummholz mats, grow in dense patches, and are capable of vegetative reproduction, which is an advantageous trait in an ecotone where seedling establishment is challenging. In contrast, bristlecone pines, common to ATE study areas in California and the Great Basin, typically exist as isolated, upright trees that only sprout from seed and do not form krummholz mats. Bristlecone pine species include foxtail pine (*Pinus balfouriana*), common to the Sierra Nevada Mountains; the Great Basin bristlecone pine (*Pinus longaeva*), found in the Basin and Range region; and the Rocky Mountain bristlecone pine (*Pinus aristata*), found in the Southern Rocky Mountains. It is notable for this research, however, that Great Basin and Rocky Mountain bristlecone pines were not considered distinct species by Little (1971). Other trees found in the ATE, but only rarely, are yellow cedar (*Chamaecyparis nootkatensis*), subalpine larch (*Larix lyallii*), and quaking aspen (*Populus tremuloides*), which, when found in the ATE, typically grows in a shrub-like form. Shrub species used to further distinguish ATE areas for this research are listed in Table 1.1.

Common Name	**Latin Name**
Rocky Mountain maple	*Acer glabrum*
Green alder (i.e., slide alder)	*Alnus sinuata* (including *A. viridis* and *A. crispa*)
Mountain alder	*Alnus tenuifolia* (including *A. incana* and *A. rugosa*)
Common juniper	*Juniperus communis*
Creeping juniper	*Juniperus horizontalis*
Rocky Mountain Juniper	*Juniperus scopulorum*
Geyer's willow **	*Salix geyeriana*
Western mountain ash	*Sorbus scopulina*
Sitka mountain ash	*Sorbus sitchensis*

Table 1.1: Shrub species included in the ATE species composition analysis.

** Note: numerous species of willow are common to the ATE, particularly in the Rocky Mountains, but few species were described within Little's (1971) range maps. Geyer's willow was selected as an indicator because it was the species most attributable to the ATE available in this dataset.

Important caveats of the selected sample sites include: (1) the geographic distribution is not random as ATE sites are only found in a few places within the region, (2) sampling was not exhaustive as some ATE areas (e.g., Mt. Rainier) were not included in this research, and (3) study sites differ with respect to the sampling density as a consequence of the amount of ATE present at each site. These issues are significant because they influence statistical approaches applicable to this dataset and/or the interpretability of results. However, despite its limitations, the dataset used for this research contains a combination of detail and a geographic range that exceeds previous ATE studies.

1.5.0. Research Outline

The research questions addressed in this dissertation are: (1) How do relationships between ATE elevation and hypothesized environmental controls vary with scale from the hillslope to the region?, (2) What environmental variables are associated with the presence of trees in alpine areas and are these relationships geographically variable?, and (3) What environmental variables are associated with objectively derived treeline pattern types and how do these associations vary across space?

The context behind this multi-site and multi-scale research is that (1) unexplained variance in higher-level models (e.g., regression residuals) is related to the spatial structure at finer scales; (2) the relative control that abiotic variables exert on the alpine treeline ecotone is scale-dependent; (3) fine grain pattern-process relations define treeline behavior and mechanisms, whereas coarse grain pattern-process relations define treeline constraints and context; and (4) characteristics of vegetation pattern may reflect the underlying constraints on treeline position. Additionally, this work will demonstrate innovative techniques for coupling biogeography, field methods, GIS, and remote sensing methodologies. Finally, this research will provide empirical evidence of the theoretical principles linking complexity and spatial scale; and relationships between vegetation pattern and environmental processes over broad geographic, geomorphic, and ecological conditions.

The general methodological approaches that are used to answer these questions are statistical and spatial analyses of scale-dependent and geographically variable relationships between ATE controls and treeline characteristics. ATE samples for this research are derived from remotely sensed imagery including air photos and Landsat TM and ETM+ satellite imagery. Hypothesized environmental controls are derived from digital elevation models and modeled climate data. Validation information for the datasets was acquired using field data collection approaches. Analyses of ATE vegetation patterns utilize the same environmental variable datasets for all study sites, but also include more in-depth analyses in the primary study sites.

1.5.1 Chapter 2 Overview

Chapter 2 of this dissertation describes and compares physical attributes of the ATE in the five primary study sites based on empirical data collected in the field. The field-based metrics of ATE character are then compared with analogous metrics derived from digital data sources to identify important similarities and differences in these measures and assess their relevance to treeline characteristics. Collected field data include (1) the location of trees and tree patches within the ATE, ranging from the edge of the closed canopy subalpine forest to uppermost isolated trees in the ecotone; (2) the fundamental landcover type adjacent to each tree or tree patch (i.e., bare rock or vegetation such as tundra, alpine meadows, or avalanche path vegetation); (3) local topographic variables including slope angle, slope aspect, and slope shape (i.e., curvature); (4) evidence of flagged trees and the apparent direction of prevailing winds; (5) an approximate tree height for each tree or tree patch; (6) a qualitative assessment of tree or tree patch growth form, ranging from prostrate krummholz trees to upright trees similar from those in the subalpine forest; (7) leaf area index values; and (8) tree species composition. These variables serve several purposes within this dissertation, most notably by (1) providing empirical evidence detailing the quality of measures derived from digital sources, (2) serving as training data for classification and visual interpretation of remotely sensed imagery, and (3) providing vital observational data with which to interpret results from statistical analyses.

1.5.2 Chapter 3 Overview

Chapter 3 of this dissertation answers the research question "How do relationships between ATE elevation and hypothesized environmental controls vary with scale from the hillslope to the region?" The general hypothesis for this research is that environmental variables are significantly correlated with treeline elevation at scales similar to those identified by Holtmeier and Broll (2005) (Figure 1.2). The overall pattern shown in Figure 1.2 suggests that global-to-regional scale controls are principally climatic while fine scale controls are largely topographic. What the graphic does not show are (1) any definition of the qualitative scales (e.g.., global and regional) and their geographic extent, and (2) an indication of the relative importance of variables at each scale of analysis. This Chapter provides empirical evidence describing the relationships between ATE elevation and specific hypothesized environmental controls at multiple spatial scales.

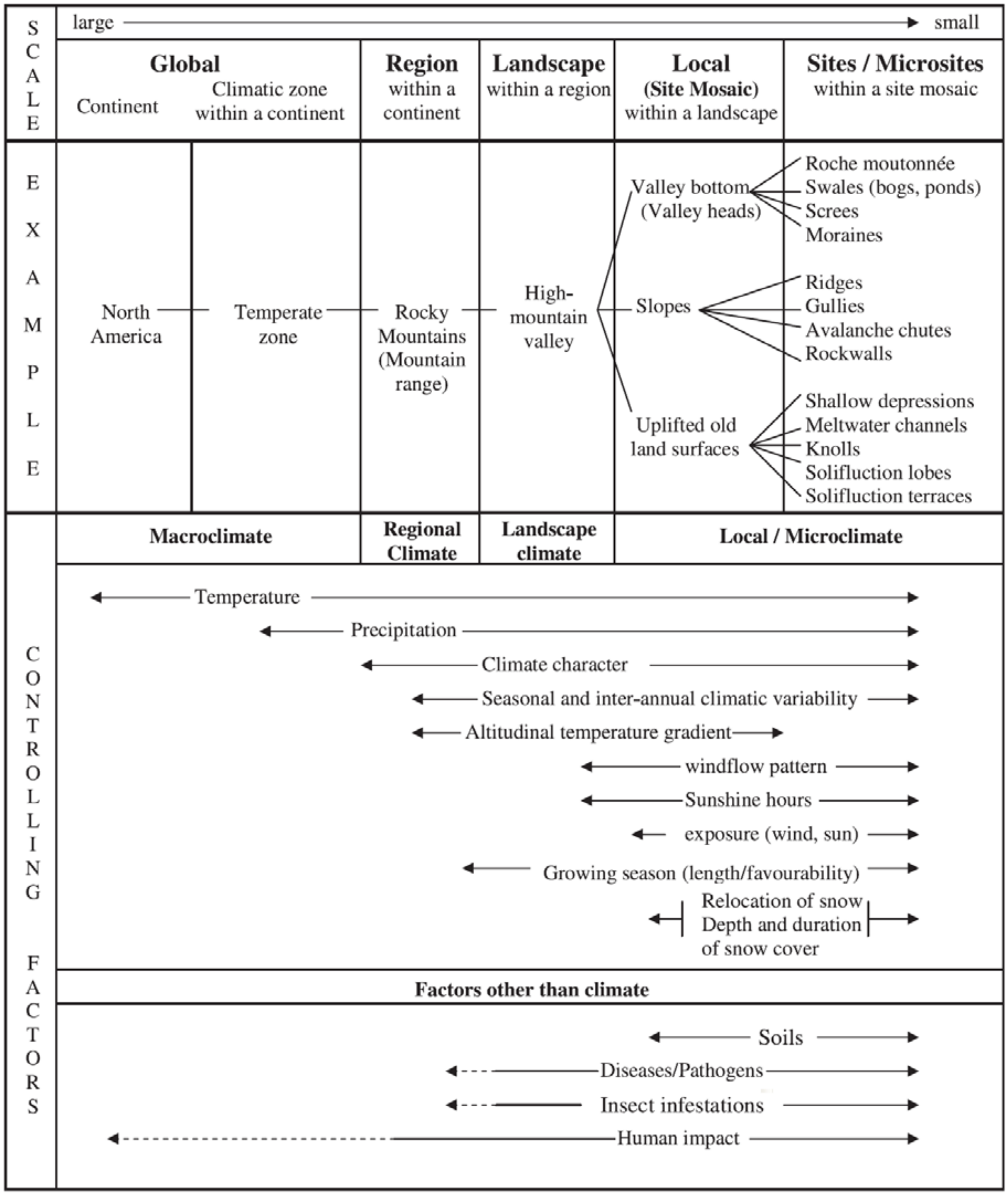


Figure 1.2: Treeline-controlling factors at different scales (Holtmeier and Broll 2005).

To answer the research question posed in Chapter 3, treeline elevation is correlated with environmental characteristics for a set of belt-transect ATE samples captured from remotely sensed imagery. The statistical approach selected for this analysis is the partial Mantel test (Legendre and Fortin 1989, Mantel 1967), in which treeline elevation and a set of environmental variables approximating controls outlined by Holtmeier and Broll (2005) are the dependent and independent variables, respectively. Table 1.2 shows the set of independent variables used in analyses for this and subsequent Chapters, descriptions of their ecological relevancy for the ATE, and the source data set from which these data are produced. The dependent and independent variables tested in Mantel tests are distances (i.e., differences in measures for each variable) between each sample point and all other sample points in the data. The distance values are arranged in vectors representing the dependent and independent variables. The overall test of significance is obtained by comparing the Mantel test statistic (the Mantel r) derived from the original distance vectors to the test statistics derived from thousands of tests in which the values of one of the distance vectors are randomized (Legendre and Legandre 1998). Partial Mantel tests allow the effect of a single independent variable to be measured while controlling for other independent variables. The advantage of partial Mantel tests for ecological research is that they can explicitly incorporate space within the analysis by including geographic distance as an independent variable. Therefore, the direct effect of space can be analyzed, as well as the effects of independent variables when controlling for space. This is a key feature because spatial autocorrelation can distort regression results derived from ecological data. Another challenge for this analysis is the presence of multicollinearity among the independent environmental variables. To account for multicollinearity, selected environmental variables were deleted from the analyses based upon the variance inflation factor threshold described in Hair et al. (2006).

Independent Variable	Ecological Significance	Source
Mean Annual Shortwave Radiation *	Modeled estimates for the total amount of shortwave radiation incident upon each ATE sample. This measure is indicative of the total amount of incident solar energy, which is a fundamental control on temperature.	Daymet
Mean Annual Precipitation *	The total annual volume of precipitation falling at each ATE sample. Precipitation at the ATE falls predominately as snow, which may benefit trees by providing winter insolation, but may also hinder trees by shortening the length of the growing season	Daymet
Annual Precipitation Standard Deviation *	A measure of the interannual variability in total precipitation. This measure is relevant because increased variability exposes trees in the ATE to a wider range of climate stresses (e.g., moisture limitations, lack of winter insolation, and shortened growing season length) that may exceed the tolerance of even the hearty species that grow in the ecotone.	Daymet
Elevation **	Elevation is directly related to temperature in alpine environments because (1) rising air expands and cools in response to decreasing air pressure, (2) higher elevation areas have less atmosphere above them to provide insolation, and (3) most sensible heat is derived from thermal radiation emanating from the land surfaces, and there is less land area present with increasing elevation as peaks become fewer and more isolated. Elevation is also relevant as relative humidity and CO_2 concentrations decrease with altitude.	DEM
Slope Angle	Steep slopes may preclude the establishment of trees through instability (e.g., mass movements), inadequate soils, high rates of erosion, and relatively dry conditions resulting from rapid runoff of moisture.	DEM Derivative

Slope Aspect (cosine, sine, and transformed)	Slope aspect affects plants at the ATE because the intensity of solar energy is controlled by the surface aspect relative to the sun angle. This effect is more pronounced in high latitudes where sun angles are lower, thereby creating greater differences between slopes in sunlight and those in shadow. Slope aspect is also relevant in the ATE as it influences the redistribution of snow (i.e., scouring from windward slopes and drifting on leeward ones). Incident solar energy and snow redistribution both influence soil moisture conditions.	DEM Derivative
Topographic Curvature (plan, profile, and total)	Topographic curvature influences the redistribution of snow as convex areas tend to have thinner snow-packs compared to concave areas. This phenomenon is a result of snow accumulation in sheltered areas and removal from exposed areas. At longer time scales, these variables are also relevant for the accumulation or removal of materials susceptible to erosion by wind and water.	DEM Derivative
Topographic Wetness Index	The relative soil moisture (within a study area) that is calculated as a function of upslope accumulation area and slope steepness. This measure has particular utility for the ATE in areas where moisture stress may be a limitation on tree establishment and/or growth.	DEM Derivative
Species Compositional Similarity	Species composition may influence the maximum elevation at which trees grow due to differences in the physiological tolerances of ATE species and/or facilitative relationships between groups of species.	Species Range Maps (Little 1971)

Table 1.2: Variables used in the analysis of treeline elevation, tree presence, and pattern.

* Climatic variables from Daymet are used in Chapter 3, and only for analyses at scales coarse enough to exclude sites from the same study areas (i.e., those sites for which meteorological data were modeled using the same base station data).

** Elevation is used as the dependent variable in Chapter 3, but as an independent variable in Chapters 4 and 5.

Scaled simple and partial Mantel tests are used to answer the research question posed for this Chapter. Simple Mantel tests are used to show the relationships between single independent and dependent variables. In contrast, partial Mantel tests are used to show the relationships between single independent and dependent variables after controlling for the effects of other independent variables. For example, a partial Mantel test is used to show the relationship between ATE elevation and slope aspect after controlling for many other topographic and climatic variables. The analyses for this Chapter are further divided into two distinct scales, as modeled climate results require meteorological base station data as inputs, and therefore sites close together will lack independence due to their reliance on identical source datasets. The scaled component of Mantel tests involves first separating the input dataset into classes according to geographic distance, and then assessing the relationships of interest at several spatial scales. The results from scaled Mantel tests are graphs showing the Mantel correlation at each scale of analysis.

1.5.3 Chapter 4 Overview

Chapter 4 addresses the research question "What environmental variables are associated with the presence of trees in alpine areas and are these relationships geographically variable?" Environmental variables to be tested in this analysis include elevation, slope aspect, slope angle, slope curvature, and topographic wetness index. Tree presence within the ATE is hypothesized to have the strongest relationship with elevation, as this variable is directly associated with temperature. Other variables, however, are also expected to influence tree presence as they influence micro-climatic effects that may facilitate or preclude tree establishment or growth within the ecotone.

This Chapter will focus on geographic variability in relationships between tree presence and environmental variables hypothesized to influence the ATE. Spatial scale will be explored using logistic regression models derived for entire National Park study areas, as well as for logistic Geographically Weighted Regression (GWR) models that assess intra-Park variability. Geographic variability will be explored by comparing and contrasting results from each study area that are generated using a consistent methodological framework and matching source datasets. Hypotheses tested within Chapter 4 include: (1) at fine spatial scales the relationship between elevation and tree presence will decrease as other topographic variables become more important due to their creation of localized micro-climatic effects, (2) elevation has a stronger relationship with tree presence in treelines controlled primarily by climatic limitations (i.e., those not limited by structural constraints such as sheer cliffs), (3) important geographic differences exist in the relationship between ATE tree presence and slope aspect in response to volume and type of snow falling at each site, as well as its propensity to be redistributed by wind, (4) the probability of tree presence increases on south and southwest facing slopes that tend to be warmer and have longer growing seasons compared to slopes with different aspects.

The methodological approaches used to address the research question posed in this Chapter are simple logistic regression, multiple logistic (stepwise) regression, and logistic GWR. The general intent is to assess the ATE samples in stages whereby the relationships between ATE presence/absence and the hypothesized control variables are examined in different geographic arrangements and at different spatial scales. GWR adheres to this analytical framework by deriving individual regression models at each sample point, with the values for the independent and dependent variables for all other samples inversely weighted according to their distance from the initial sample (Fotheringham et al. 2002). The results from the GWR analysis will be mapped to graphically demonstrate how ATE controls vary with space across the western United States.

1.5.4 Chapter 5 Overview

Chapter 5 of this dissertation addresses the research question, “What environmental variables are associated with treeline pattern types and how do these associations vary with space?” This Chapter also answers sub-questions, “can alpine treeline vegetation patterns be clustered into a typology that is a robust classifier of treeline pattern at all study sites” and “Is there evidence to support the idea that treeline patterns are polygenic in nature?” Patterns likely to emerge include abrupt treelines, wide ecotones with an open canopy structure, and several types of wide ecotones characterized by different patch size and shape relationships. Because the environmental conditions at the ATE vary greatly with space, so too will their associations with treeline pattern. The reoccurrence of similar treeline patterns in very different environments will support the idea that treeline patterns are polygenic.

The relationships between environmental variables and ATE patterns are expected to generally follow the simple treeline typology established by Holtmeier (2003) that describes alpine treelines as either climatically- or orographically- (i.e., topographically) controlled. The hypothesized ATE controlling variables expected to separate these two classes are primarily topographic because trees grow to their climatic limit unless some other factor(s) prevent them from doing so. Abrupt treeline ecotones are expected to associate with orographic controls, in particular slope angle and additional variables captured when summarizing slope angle values for belt-transect ATE samples (e.g., abrupt slope changes such as cliffs). Topographic variables influencing the redistribution of snow, such as slope aspect and slope curvature, are also expected to influence treeline characteristics and potentially contributing to orographic treelines. Species compositional differences also affect ATE patterns as the life strategies of some tree species favor growing in dense patches, while other species grow independently. These different tree life strategies are particularly relevant in the ATE because tree growth forms can produce feedbacks that affect snow redistribution (e.g., snow drift size). Another variable expected to affect treeline type is geologic substrate, as resistant rocks are likely to provide a more uniformly stable surface on which soils can develop and trees can grow.

The methods used to answer the research question in Chapter 5 include the derivation of landscape pattern metrics from classified satellite imagery, cluster analysis, simple descriptive statistics, and Classification And Regression Trees (CART) (Breiman et al. 1984). The data source for these analyses is classified Landsat imagery, which limits the pattern analyses to a single spatial scale (i.e., 30 x 30 meter pixels). This spatial scale is appropriate for this analysis, however, as the independent variables are derived primarily from DEMs with comparable spatial resolutions. In this analysis, landcover patterns for ATE samples in all 26 study sites are derived from simple landcover classifications (i.e., coniferous trees; other vegetation including tundra and riparian; bare rock, snow, and ice; and water). A set of pattern metrics is derived for each ATE belt-transect sample using FRAGSTATS (McGarigal and Marks 1995). The pattern metrics selected for this analysis follow the suggestions of Riitters et al. (1995). Pattern metric selection also incorporates theoretical understanding of treeline dynamics to better characterize the spatial arrangement of patches (in this case trees and tree clusters). ATE types are derived by applying cluster analysis to the pattern metric results. Environmental characteristics are attributed to the resulting clusters using simple descriptive statistics applied to the full set of clusters and to spatial subsets of clusters for only the primary study sites. This split methodology addresses spatial differences in the environmental characteristics associated with each type. Lastly, CART analysis is used to determine the environmental variables most effective for predicting the ATE pattern. As with the simple descriptive statistical analyses, CART is applied to both the full set of samples, and subsets based on sample site.

1.6.0 Conclusion

ATE controls vary with space and scale as the underlying abiotic template, in particular climatic gradients, changes at multiple spatial scales. This dissertation addresses several aspects of the spatial and scalar variability of the ATE in the western United States by exploring the relationships between ATE characteristics and environmental variables hypothesized to influence the ecotone. The results of this research increase the understanding of ATE dynamics, particularly at regional scales, where empirically based analyses are rare. The results of this research are also potentially useful for climate change researchers because, like ATE controlling factors, the effects of climate change are geographically variable. Therefore, effectively predicting how and where ATE characteristics will change requires a thorough understanding of the spatial patterns of ATE controls. Merging climate change predictions with ATE controls will increase the utility of the ATE as a bellwether of climate change impacts. Lastly, understanding the patterns of relationships between ATE characteristics and hypothesized controls is useful for mapping ATE areas that are sensitive to infilling and/or upslope advance.

This research fits into the broader field of ecotone studies by exploring geographic variability and scale-dependencies inherent to pattern-process relationships within a dynamic ecotone. Within the framework of Gosz (1993), the analyses conducted within this dissertation are based upon data collected at the patch-to-landscape scales, but what sets this research apart from previous endeavors is that it is designed to directly compare treeline ecotones dispersed across a region using a standardized methodology. Within the framework of Strayer et al. (2003), Chapters 3 and 4 of this dissertation explore the origin and maintenance of the ATE, while Chapter 5 examines the spatial structure of the ATE within the selected study sites. Much like the afore-mentioned ecotone classification systems, the utility of this research lies primarily in its ability to provide a context in which previous ATE research can be compared. Furthermore, this research has the potential to inform studies focused on ATE reactions to climate change, particularly with respect to spatial variability in these responses.

1.7.0 References

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

Allen, C. D., and D. D. Breshears. 1998. Drought-induced shift of a forest-woodland ecotone: Rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences of the United States of America* 95: 14839-14842.

Allen, T. F. H., and T. B. Starr. 1982. *Hierarchy: perspectives for ecological complexity*. The University of Chicago Press, Chicago.

Allen, T. R. 1995. Relationships between spatial pattern and environment at the alpine treeline ecotone, Glacier National Park, Montana. Pages 276. *Department of Geography*. University of North Carolina, Chapel Hill.

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

Arris, L. L., and P. S. Eagleson. 1989. Evidence of a physiological basis for the boreal-deciduous forest ecotone in North America. *Vegetatio* 82: 55-58.

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

—. 1997. Using GIS to model tree population parameters in the Rocky Mountain National Park forest-tundra ecotone. *Journal of Biogeography* 24: 513 - 526.

Baron, J. S., M. D. Hartman, L. E. Band, and R. B. Lammers. 2000. Sensitivity of a high-elevation Rocky Mountain watershed to altered climate and CO2. *Water Resources Research* 36: 89-99.

Baron, J. S., D. S. Ojima, E. A. Holland, and W. J. Parton. 1994. Analysis of nitrogen saturation potential in Rocky-Mountain tundra and forest - Implications for aquatic systems. *Biogeochemistry* 27: 61-82.

Batllori, E., J. J. Camarero, J. M. Ninot, and E. Gutierrez. 2009. Seedling recruitment, survival and facilitation in alpine Pinus uncinata tree line ecotones. Implications and potential responses to climate warming. *Global Ecology and Biogeography* 18: 460-472.

Baumeister, D., and R. M. Callaway. 2006. Facilitation by Pinus flexilis during succession: A hierarchy of mechanisms benefits other plant species. *Ecology* 87: 1816-1830.

Bekker, M. F. 2005. Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, U.S.A. *Arctic, Antarctic, and Alpine Research* 37: 97-107.

Bian, L., and S. J. Walsh. 1993. Scale-dependencies of vegetation and topography in a mountainous environment of Montana. *Professional Geographer* 45: 1-11.

Billings, W. D. 1973. Arctic and alpine vegetations: Similarities, differences, and susceptibility to disturbance. *BioScience* 23: 697-704.

—, ed. 1979. *High Mountain Ecosystems*. American Association for the Advancement of Science. AAAS Selected Symposia Series. Westview Press, Inc., Boulder, CO.

Breiman, L., J. Friedman, C. J. Stone, and R. A. Olshen. 1984. *Classification and regression trees*. Chapman & Hall, New York, N.Y.

Breshears, D. D., N. S. Cobb, P. M. Rich, K. P. Price, C. D. Allen, R. G. Balice, W. H. Romme, J. H. Kastens, M. L. Floyd, J. Belnap, J. J. Anderson, O. B. Myers, and C. W. Meyer. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America* 102: 15144-15148.

Brown, D. G. 1992. Topographical and biophysical modeling of vegetation patterns at alpine treeline. Pages 239. *Department of Geography*. University of North Carolina, Chapel Hill.

—. 1994a. Comparison of vegetation–topography relationships at the alpine treeline ecotone. *Physical Geography* 15: 125– 145.

—. 1994b. Predicting vegetation types at treeline using topography and biophysical disturbance variables. *Journal of Vegetation Science* 5: 641-656.

Brown, D. G., D. M. Cairns, G. P. Malanson, S. J. Walsh, and D. R. Butler. 1994. Remote sensing and GIS techniques for spatial and biophysical analyses of alpine treeline through process and empirical models. Pages 453-481 in W. K. Michener, Stafford, S. and Brunt, J., ed. *Environmental Information Management and Analysis: Ecosystem to Global Scales*. Taylor and Francis, Pennsylvania.

Bunn, A. G. 2004. Temporal and spatial patterns at alpine treeline in the Sierra Nevada, USA: implications for global change. Pages 172. *Land Resources and Environmental Sciences*. Montana State, Bozeman, Montana.

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

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

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

Butler, D. R., G. P. Malanson, and D. M. Cairns. 1994. Stability of alpine treeline in Glacier National Park, Montana, U.S.A. . *Phytocoenologia* 22: 485-500.

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

Butler, D. R., and S. J. Walsh. 1994. Site characteristics of debris flows and their relationship to alpine treeline. *Physical Geography* 15: 181-199.

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

Cairns, D. M., and J. Moen. 2004. Herbivory influences tree lines. *Journal of Ecology* 92: 1019 - 1024.

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

Cilliers, P. 1998. *Complexity and postmodernism: Understanding complex systems*. Routledge, London.

Clements, F. E. 1907. *Plant Physiology and Ecology*. Henry Holt, New York.

Connell, J. H., and R. O. Slayter. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111: 1119–1144.

Daniels, L. D., and T. T. Veblen. 2003. Regional and local effects of disturbance and climate on altitudinal treelines in northern Patagonia. *Journal of Vegetation Science* 14: 733-742.

Delcourt, P. A., and H. R. Delcourt. 1992. Ecotone dynamics in space and time. Pages 19-54 in A. J. Hansen and F. di Castri, eds. *Landscape Boundaries: Consequences for Biotic Diversity and Landscape Flows*. Springer Verlag, New York.

Fotheringham, A. S., C. Brunsdon, and M. Charlton. 2002. *Geographically Weighted Regression : The Analysis of Spatially Varying Relationships*. Wiley, Chichester.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. *Environmental Management* 10: 199 - 214.

Gause, G. F. 1964. *The Struggle for Existence*. Hafner, New York.

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

Gosz, J. R. 1992. Gradient analysis of ecological change in time and space - Implications for forest management. *Ecological Applications* 2: 248-261.

—. 1993. Ecotone Hierarchies. *Ecological Applications* 3: 369-376.

Grinnell, J. 1917. Field tests of theories concerning distributional control. *American Naturalist* 51: 115–128.

Hair, J. F. J., W. C. Black, B. J. Babin, R. E. Anderson, and R. L. Tatham. 2006. *Multivariate Data Analysis*. Prentice Hall, Upper Saddle River, NJ.

Harris, L. D. 1988. Edge effects and conservation of biotic diversity. *Conservation Biology* 2: 330-332.

Hofgaard, A., and B. Wilmann. 2002. Plant distribution pattern across the forest-tundra ecotone: The importance of treeline position. *Ecoscience* 9: 375-385.

Holtmeier, F. K. 2003. *Mountain Timberlines: Ecology, Patchiness, and Dynamics*. Springer, Berlin.

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

Hutchinson, G. E. 1957. Concluding remarks. Pages 415-427. *Cold Spring Harbour Symposium on Quantitative Biology*.

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

—. 1998b. Worldwide positions of alpine treelines and their causes. Pages 221-229 in M. Beniston, and Innes, J.L., ed. *The Impacts of Climate Variability on Forests*. Springer, Berlin.

—. 2003. *Alpine Plant Life: Functional Ecology of High Mountain Ecosystems*. Springer-Verlag, Berlin.

Kullman, L. 1995. Holocene tree-limit and climate history from the Scandes-Mountains, Sweden. *Ecology* 76: 2490-2502.

—. 1996. Recent cooling and recession of Norway spruce (Picea abies (L.) Karst.) in the forest-alpine tundra ecotone of the Swedish Scandes. *Journal of Biogeography* 23: 843-854.

Kullman, L., and L. Oberg. 2009. Post-Little Ice Age tree line rise and climate warming in the Swedish Scandes: a landscape ecological perspective. *Journal of Ecology* 97: 415-429.

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

Legendre, P., and M. Fortin. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80: 107-138.

Legendre, P., and L. Legandre. 1998. *Numerical Ecology*. Elsevier, Amsterdam.

Leopold, A. 1933. *Game management*. Charles Scribner, New York.

Levin, S. A., and L. A. Segel. 1976. Hypothesis to explain the origin of planktonic patchiness. *Nature* 259: 659–676.

Lidicker, W. Z. 1999. Responses of mammals to habitat edges: an overview. *Landscape Ecology* 14: 333-343.

Lingua, E., P. Cherubini, R. Motta, and P. Nola. 2008. Spatial structure along an altitudinal gradient in the Italian central Alps suggests competition and facilitation among coniferous species. *Journal of Vegetation Science* 19: 425-436.

Little, J. E. L. 1971. *Conifers and Important Hardwoods*. US Department of Agriculture, Washington, DC.

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

Macdonald, G. M., T. W. D. Edwards, K. A. Moser, R. Pienitz, and J. P. Smol. 1993. Rapid response of treeline vegetation and lakes to past climate warming. *Nature* 361: 243-246.

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

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

Malanson, G. P., and D. M. Cairns. 1997. Effects of dispersal, population delays, and forest fragmentation on tree migration rates. *Plant Ecology* 131: 67-69.

Malanson, G. P., N. Xiao, K. J. Alftine, M. F. Bekker, D. R. Butler, D. G. Brown, D. M. Cairns, D. Fagre, and S. J. Walsh. 2000. Abiotic and biotic controls of spatial pattern at alpine treeline. *4th International Conference on Integrating GIS and Environmental Modeling (GIS/EM4)*, Banff, Alberta, Canada.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27: 209-220.

McGarigal, K., and B. J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. *USDA Forest Service General Technical Report PNW-351*.

Neilson, R. P. 1993. Transient Ecotone Response to Climatic-Change - Some Conceptual and Modeling Approaches. *Ecological Applications* 3: 385-395.

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

Paulsen, J., U. M. Weber, and C. Korner. 2000. Tree growth near treeline: Abrupt or gradual reduction with altitude? *Arctic Antarctic and Alpine Research* 32: 14-20.

Peters, D. P. C. 2002. Plant species dominance at a grassland-shrubland ecotone: an individual-based gap dynamics model of herbaceous and woody species. *Ecological Modelling* 152: 5-32.

Rebertus, A. J., B. R. Burns, and T. T. Veblen. 1991. Stand dynamics of Pinus flexilis–dominated sub-alpine forest in the Colorado Front Range. *Journal of Vegetation Science* 2: 445–458.

Resler, L. M. 2006. Geomorphic controls of spatial pattern and process at alpine treeline. *Professional Geographer* 58: 124-138.

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

Ries, L., R. J. Fletcher, J. Battin, and T. D. Sisk. 2004. Ecological responses to habitat edges: Mechanisms, models, and variability explained. *Annual Review of Ecology Evolution and Systematics* 35: 491-522.

Riitters, K. H., R. V. O'Neill, C. T. Hunsaker, J. D. Wickham, D. H. Yankee, S. P. Timmins, K. B. Jones, and B. L. Jackson. 1995. A factor analysis of landscape pattern and structure metrics. *Landscape Ecology* 10: 23 - 29.

Risser, P. G. 1995. The Status of the Science Examining ecotones - a dynamic aspect of landscape is the area of steep gradients between more homogeneous vegetation associations. *Bioscience* 45: 318-325.

Rupp, T. S., F. S. Chapin, and A. M. Starfield. 2001. Modeling the influence of topographic barriers on treeline advance at the forest-tundra ecotone in northwestern Alaska. *Climatic Change* 48: 399-416.

Seastedt, T. R., W. D. Bowman, T. N. Caine, D. McKnight, A. Townsend, and M. W. Williams. 2004. The landscape continuum: a model for high-elevation ecosystems. *BioScience* 54: 111-121.

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

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

Strayer, D. L., M. E. Power, W. F. Fagan, S. T. A. Pickett, and J. Belnap. 2003. A classification of ecological boundaries. *Bioscience* 53: 723-729.

Tranquillini, W. 1979. *Physiological Ecology of the Alpine Timberline: Tree Existance at High Altitudes with Special Reference to the European Alps*. Springer-Verlag, Berlin.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* 20: 171-197.

Turner, M. G., R. V. O'Neill, W. Conley, M. R. Conley, and H. C. Humphries. 1991. Pattern and scale: Statistics for landscape ecology. Pages 17-49 in M. G. Turner and R. H. Gardner, eds. *Quantitative methods in landscape ecology*. Springer-Verlag, New York.

Urban, D. L., C. Miller, P. N. Halpin, and N. L. Stephenson. 2000. Forest gradient response in Sierran landscapes: The physical template. *Landscape Ecology* 15: 603-620.

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

Walsh, S. J., D. R. Butler, T. R. Allen, and G. P. Malanson. 1994. Influence of snow patterns and snow avalanches on the alpine treeline ecotone. *Journal of Vegetation Science* 5: 657-672.

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

Weltzin, J. F., and G. R. McPherson. 1999. Facilitation of conspecific seedling recruitment and shifts in temperate savanna ecotones. *Ecological Monographs* 69: 513-534.

Whitlock, C., M. A. Reasoner, and C. H. Key. 2002. Paleoenviromental history of the Rocky Mountain region during the last 20,000 years. Pages 41-59 in J. A. Barron, ed. *Rocky Mountain Futures: An Ecological Perspective*. Island Press, Washington.

Whittaker, R. H. 1975. *Communities and ecosystems*. Macmillan, New York.

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

Wiens, J. A., C. S. Crawford, and J. R. Gosz. 1985. Boundary dynamics - a conceptual-framework for studying landscape ecosystems. *Oikos* 45: 421-427.

Wiens, J. A., N. C. Stenseth, B. Vanhorne, and R. A. Ims. 1993. Ecological mechanisms and landscape ecology. *Oikos* 66: 369-380.

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

CHAPTER 2

COMPARISON OF FIELD-BASED MEASUREMENTS OF THE ALPINE TREELINE ECOTONE IN THE WESTERN UNITED STATES

2.1.0 Introduction

Alpine Treeline Ecotones (ATE) in the western United States exhibit dramatically different characteristics in response to diverse environmental conditions present within the region. The nature of pattern-processes relationships regulating the ATE varies across space due to non-linearities of treeline controls (e.g., threshold conditions) and interactions between variables (e.g., the relationship between wind, annual snowfall, properties of the snow, and topographic conditions all influence the redistribution of snow) (Malanson et al. 2001). The primary intent of this Chapter is to compare ATE characteristics from study areas distributed across regional climatic gradients (i.e., temperature and moisture) using identical field methodologies. Included are observed differences in the physical landscapes of the ATE, and measured as 2-and 3-dimensional responses of the ATE to geographically-variable landscape features. The secondary objective is to compare field based measures of the ATE to measures derived from digital datasets (e.g., remotely sensed imagery and Digital Elevation Models (DEM)). The intent is to assess the utility of selected digital datasets for quantifying characteristics of the ATE and its physical setting.

This Chapter utilizes *in situ* data collected at five ATE study areas that have a rich legacy of prior research. Utilizing such well described sites aids in the interpretation of derived research findings and provides a context for the comparative analysis. The results presented in this Chapter provide regional comparisons and syntheses, which are rare in analyses of the ATE.

2.2.0 Background

Numerous examples of field-based analyses of the ATE address topics related to pattern-process relationships within the ecotone. Examples include tree physiological responses to climatic conditions (e.g., Bader et al. 2007, Germino et al. 2002), geomorphic processes (e.g., Butler et al. 2004, Resler 2006, Resler et al. 2005) , disturbances (Daniels and Veblen 2003), historical positions (e.g., Bunn et al. 2005b, e.g., Butler et al. 1994, Cuevas 2000, Kullman 1996), vegetation productivity (e.g., Paulsen et al. 2000), soil conditions (e.g., Cairns 1999, Holtmeier and Broll 1992, Malanson et al. 2002), feedback effects (e.g., Bekker 2005), seedling establishment (e.g., Batllori et al. 2009, e.g., Cuevas 2000, Moir et al. 1999), and other processes and conditions hypothesized to affect the ATE. These analyses tend to focus on relationships between biotic characteristics and abiotic conditions, in particular how biota respond to environmental settings at various spatial scales (e.g., through spatial patterns of tree presence/absence) (e.g., Bader and Ruijten 2008, Brown 1994b), structural changes in plant growth forms (e.g., krummholz vs. upright trees), or feedback processes that alter micro-site conditions for species or communities in the ecotone (e.g., Bader et al. 2008, Wilson et al. 1993). What is typically absent from such field-based studies is a synthesis across geographic space, as analyses tend to be restricted to small, intensively sampled study areas.

The use of metrics derived from digital sources is common within ATE research as these datasets can greatly expand the geographic scope of analyses in areas where complex terrain and limited accessibility make fieldwork challenging. One common approach is to link *in situ* measurements with those derived from remotely sensed imagery (1) through classification validations (e.g., Allen and Walsh 1996), (2) by associating vegetation indices with topographic conditions (Walsh et al. 1997) or ground based measurements such as Leaf Area Index (LAI) (Brown 2001), and (3) as inputs into statistical models that assess and/or predict ATE landcover patterns (Bader and Ruijten 2008, Brown 1994b, Cairns 2001). Studies that utilize remotely–sensed imagery to analyze the ATE over coarse areas (i.e., at scales impractical for field-based approaches) typically utilize environmental covariates derived from DEMs. Many of these variables are also utilized as inputs for ecosystem process models that explore ATE productivity and temporal dynamics (e.g., Alftine and Malanson 2004, Malanson et al. 2001, Scuderi et al. 1993).

Despite the widespread use of environmental covariates derived from raster datasets such as DEMs within statistical and mechanistic models, published ATE research utilizing such datasets is seldom accompanied by a discussion of the relative quality of these data, particularly when used for measuring topographic characteristics within complex terrain. This is an understandable omission in many cases, as medium resolution DEMs (e.g., 10- or 30-meter USGS datasets that are easily obtained for the continental U.S.) closely match the spatial resolution of the other commonly used datasets (e.g., Landsat imagery) (Brown et al. 1994). However, the importance of fine scale conditions and processes (e.g., microclimatic effects) on ATE patterns and dynamics, as well as the increasing availability of high spatial resolution remotely sensed imagery, provides the impetus to reassess the utility of existing DEMs for detailed analyses of treelines.

2.3.0 Study Area

The study areas for this research consist of five National Parks in the western United States that are located in very different geographic settings. Two of the Parks, Rocky Mountain National Park (RMNP), Colorado, and Glacier National Park (GNP), Montana, are located in the Rocky Mountains and feature primarily continental climate regimes. Notable differences between these Parks include (1) latitude, and therefore temperature, as RMNP is located approximately eight degrees south of GNP, and (2) geologic substrate, with RMNP being dominated by granitic rocks and GNP underlain by predominately sedimentary strata. Further west are the study areas of North Cascades National Park, Washington (NCNP), and Sequoia National Park, California (SNP). Although these study areas are located in different mountain ranges (i.e., the North Cascades and Sierra Nevada ranges, respectively), they share similar characteristics such as (1) significant quantities of resistant igneous and metamorphic substrate coincident with the ATE, and (2) locations in the first major mountain range east of the Pacific Coast at their respective latitudes. Therefore, in comparison to the continental study areas, NCNP and SNP receive more precipitation in response to (1) local orographic lifting of moist Pacific air masses, and (2) the lack of a regional rain shadow effect whereby Pacific air masses are comparatively dry when they reach mountains farther inland. The final study area is Olympic National Park (ONP), Washington. This site is located on the Olympic Peninsula, is immediately adjacent to the Pacific Ocean, and receives more precipitation than the other study areas. ONP also features more variable geologic conditions than the other study areas.

With respect to ATE tree species composition, RMNP and GNP have essentially the same set of dominant species (i.e. Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*)). ONP and NCNP have a species composition fairly similar to RMNP and GNP, although Engelmann spruce is comparatively rare and mountain hemlock (*Tsuga mertensiana*) is much more prominent within treelines in these Parks. The ATE in SNP, in contrast, is dominated by foxtail pine (*Pinus balfouriana*), and characteristics of this species are responsible for producing important differences in spatial patterns and pattern-process relationships at treeline. For more in-depth descriptions of these study areas, see Chapter 1.

2.4.0 Methods – Sampling Design

Study areas for this research include the five National Parks mentioned above. Within each study area several study sites were selected from which sample points were collected. Study sites were selected opportunistically within the National Park study areas, but care was taken to sample varying types of ATEs (e.g., climatically- and orographically-controlled treelines). Study site selection was also designed to capture ATE conditions across a range of slope angle and slope aspects (Figure 2.1). Study sites were selected to coincide with the footprint of high spatial resolution satellite imagery acquired for this research. However, due to limited potential study sites within these images, some data points were collected in other ATE areas to produce a more complete sample of Park-wide ATE conditions. Some study areas are in relatively close proximity to each other (i.e., < 1 km), but the spatial areas from which samples were collected do not overlap. Sample points within each study site were selected to span the vertical range of the ecotone as they extend from the edge of the closed-canopy subalpine forest to the uppermost tree in the ecotone. Each sample point contains the full set of field data collected for this analysis, and the consistency of methods was maintained.

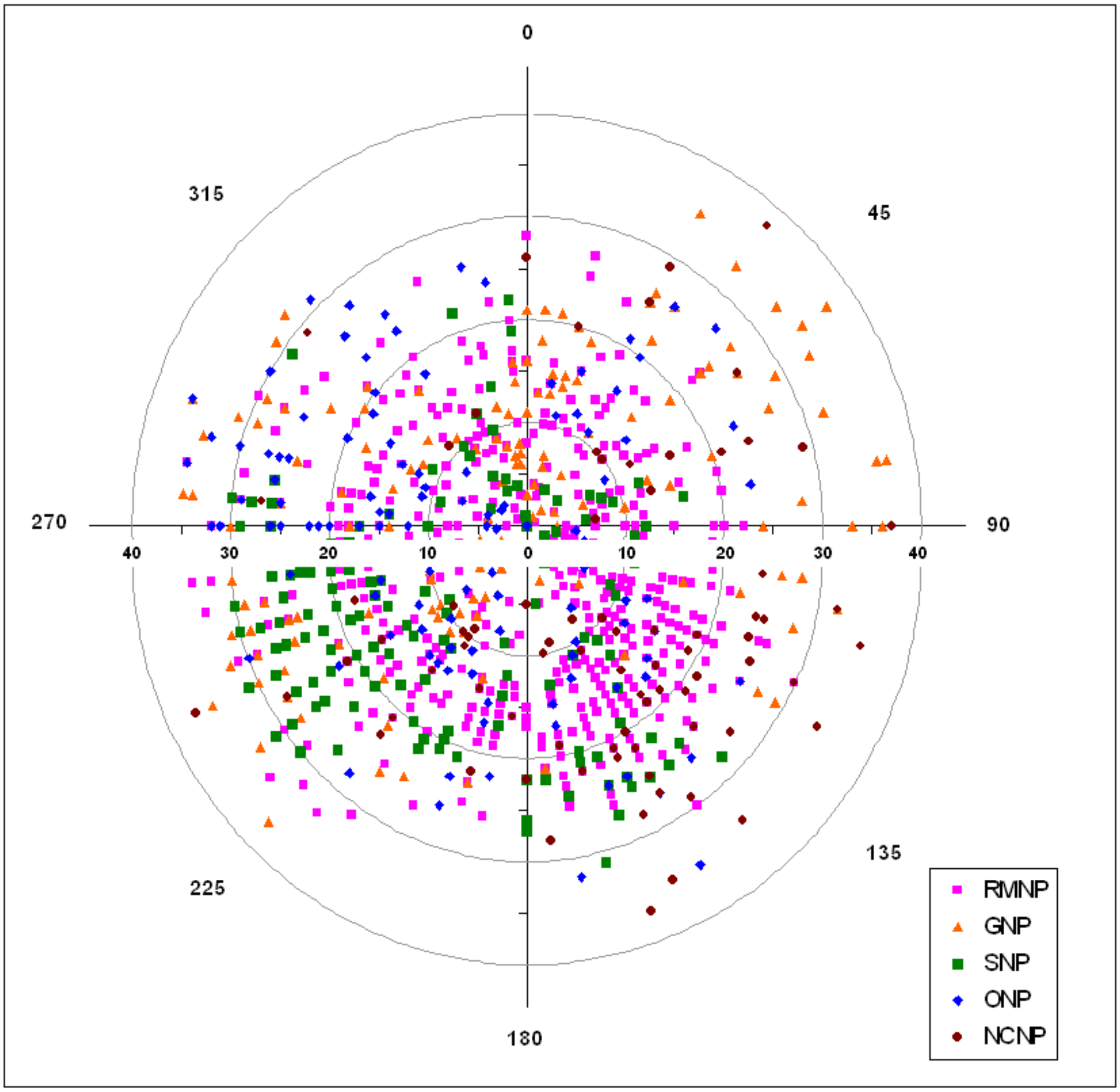


Figure 2.1: Slope angle and slope aspect distribution of the sample points. Slope angle is indicated by the distance from the center of the graph, with each ring indicating 10 degrees. Slope aspect is indicated by the angle from the center point, with compass bearings provided around the circle for reference.

A total of 1,018 points were collected from the five study areas. From this set, 21 points were deleted due to GPS errors, leaving a final sample size of 997 points within the ATE study areas. The spacing of the sample points within a single study site was consistently applied (i.e., 30-50 meters separated consecutive points, although in areas with few krummholz patches, sample spacing was determined by patch availability), and 20 to 25 points were typically collected at each site. The spatial distribution of the sample points was determined by the 2-D structure of the ecotone. In abrupt ecotones, sample points were collected along a line that was roughly parallel to the abrupt edge. In contrast, wider ecotones had a rectangular shaped sampling design, with roughly parallel transects collected in the lower and upper portions of the ecotones, plus several points in intermediate areas. Table 2.1 details the distribution of sample points collected in each study area. All study areas had at least 80 points collected for use in regional scale analyses. Differences in the sampling intensity across sites occurred as a results of time constraints, meteorological conditions, and logistical challenges that made some Parks much easier to sample than others.

Study Area	Study Sites	Total Points Collected	Points Coincident With Ikonos Imagery
RMNP	23	492	487
GNP	7	166	94
NCNP	4	80	80
SNP	8	132	77
ONP	7	127	55
Total	49	997	793

Table 2.1: Distribution of usable sample points within each study area.

An important consideration associated with this dataset is the non-random nature of the ATE samples that results from an opportunistic sampling design influenced by access, terrain, and available ATE types. When coupled with qualitative observations, however, these data can support previous ATE research findings and help provide at least a description of major differences between study areas. Such descriptions are useful as contextual information for subsequent Chapters in this dissertation. The advantage of this sampling approach is that it captures a wide range of ecotone types and features that might not be as well sampled using a random approach, especially in study areas where great effort is required to reach remote sample sites. Particularly useful components of this dataset are tree height measurements and adjacent landcover types that will be examined in subsequent analyses.

2.4.1 Methods – Data Collection

The following measurements and observations were collected at each sample point:

(1) The location of trees and tree patches within the ATE, ranging from the edge of the closed canopy subalpine forest to the uppermost, isolated trees in the ecotone. Tree locations were defined using a GPS unit and Earth coordinates that were collected at each sample point. All GPS measurements were differentially corrected for improved accuracy.

(2) The fundamental landcover type adjacent to each tree or tree patch (i.e. bare rock or vegetation). Adjacent landcover was visually assessed on a scale from 1 to 4, with 1 being dominated by rock; 2 indicating both landcover types were present, but rock in a greater proportion; 3 indicating both landcover types were present, but vegetation in a greater

proportion; and 4 being predominately vegetation. For reference, labeling adjacent landcover as "vegetation" required the presence of short, herbaceous plants like those found in alpine tundra and alpine meadows. This distinction was made because woody stemmed species, including shrubs such as Rocky Mountain maple (*Acer glabrum*), occasionally grow within or immediately adjacent to trees or tree patches. Within the framework of this analysis, shrub species were considered to be trees, and therefore part of the ATE tree patch, as their growth form and stature are similar to that of krummholz trees.

(3) Variables describing the local topographic setting of each sample point, including slope angle, slope aspect, and slope shape (i.e., curvature). Slope angle was estimated using a clinometer, slope aspect was estimated visually and measured with a compass, and slope curvature was assessed visually and attributed to one of the six following categories: concave, slightly concave, convex, slightly convex, hummocky, or flat.

(4) Evidence of flagged trees and the apparent direction of prevailing winds. Flagged trees were identified visually and a compass bearing was taken to assess the prevailing (winter) wind direction (i.e., the direction opposite the flagged vegetation).

(5) An approximate tree height for each tree or tree patch. Tree height was estimated visually with the help of a marked 2.6 meter pole placed in or adjacent to trees or tree patches. Estimates were used rather than exact measurements because tree patches are typically comprised of many trees that have unequal heights, and an average, representative height was appropriate for analyses at the scale of the patch. For vegetation under 2.4 meters tall, an actual measurement was collected, and for taller trees the measurement pole was useful for judging height. This approach caused the uncertainty of the height measurements to increase with increasing tree height, but quantifying heights of trees taller than 4 meters was not as critical for this research as tall trees are unlikely to be relying on feedbacks that are potentially vital for smaller trees within the ATE (Körner 2003). Furthermore, tree heights are placed into a limited number of height classes for analysis, and the estimated heights are judged to be sufficiently accurate for such an approach.

(6) An estimate of tree patch size relative to the spatial resolution of imagery collected for the study areas. Tree patch size was estimated visually as being clearly larger than, clearly smaller than, or approximately equal to the size of a 4X4 meter Ikonos multispectral pixel.

(7) A qualitative assessment of tree or tree patch growth form, ranging from prostrate krummholz trees to upright trees similar to those in the subalpine forest (note: this measure was only collected in RMNP and GNP where krummholz is commonly found). Tree growth form was visually assessed using the following definitions: (1) obvious krummholz, including a dense and uniform upper layer of needles; (2) krummholz with one or more pioneer stems projecting above the upper needle layer, these stems were typically flagged and/or had few green needles; (3) several upright stems with remaining foliage projecting above a dense needle layer; (4) primarily upright trees, with evidence of previous krummholz forms (e.g., gnarled trunks often growing parallel to the ground at the base); (5) upright trees without evidence of past krummholz forms, but significantly shorter than trees found down slope and often possessing flagging on upper branches; and (6) upright trees essentially indistinguishable from their subalpine forest counterparts except for their position at or above the forest edge.

(8) Leaf area index values. These values were collected using an LAI-2000 plant canopy analyzer that measures the canopy gap fraction present in vegetation, as determined using the ratio of light measurements taken above and below foliage. The LAI-2000 was designed for use in diffuse light conditions (e.g., at dawn or dusk, or on uniformly cloudy days), but

because ATE sites could not be easily reached at those times, efforts were taken to mitigate the affects of direct sunlight (e.g., the smallest lens cap was used to limit the total amount of light coming into the sensor, and measurements were always taken in the shade to avoid the influence of direct sunlight).

(9) Tree species composition. All tree and shrub species identifiable at each sample points were recorded.

(10) Field photos capturing the local conditions present at each sample point were taken in four directions (i.e., right, left, away, and back towards the GPS receiver).

These variables serve several purposes within this dissertation, most notably they (1) provide empirical evidence detailing the quality of measures derived from digital sources, (2) serve as training data for classification and visual interpretation of remotely sensed imagery, and (3) provide vital observational data with which to interpret results from statistical analyses.

2.5.0 Results - Site Comparisons and Regional Context

Several important results are shown in Figure 2.2 including (1) a graphical representation of the approximate ATE elevation in each study area, (2) an indication of the ATE elevation range present in each study area (i.e., a sense of the variance in ATE elevation), and (3) a graphical representation of the relationship between ATE elevation and tree height in each study area. Treeline elevations at sample points in the western U.S. have a range of over 2000 meters, with points from the southern study areas (i.e., RMNP and SNP) being considerably higher than points from the northern areas (i.e., GNP, ONP, and NCNP). Among the northern study areas, treeline is higher in GNP than in NCNP and ONP, despite the similar latitudes of these Parks. With respect to intra-Park variability in ATE elevation, the results suggest that treeline occurs at more consistent elevations in RMNP than the other study areas. In contrast, GNP has the most variability in measured ATE elevation. All sites demonstrate the expected negative relationship between ATE elevation and tree height. However, ATE elevation alone was a poor predictor of tree height in all study areas.

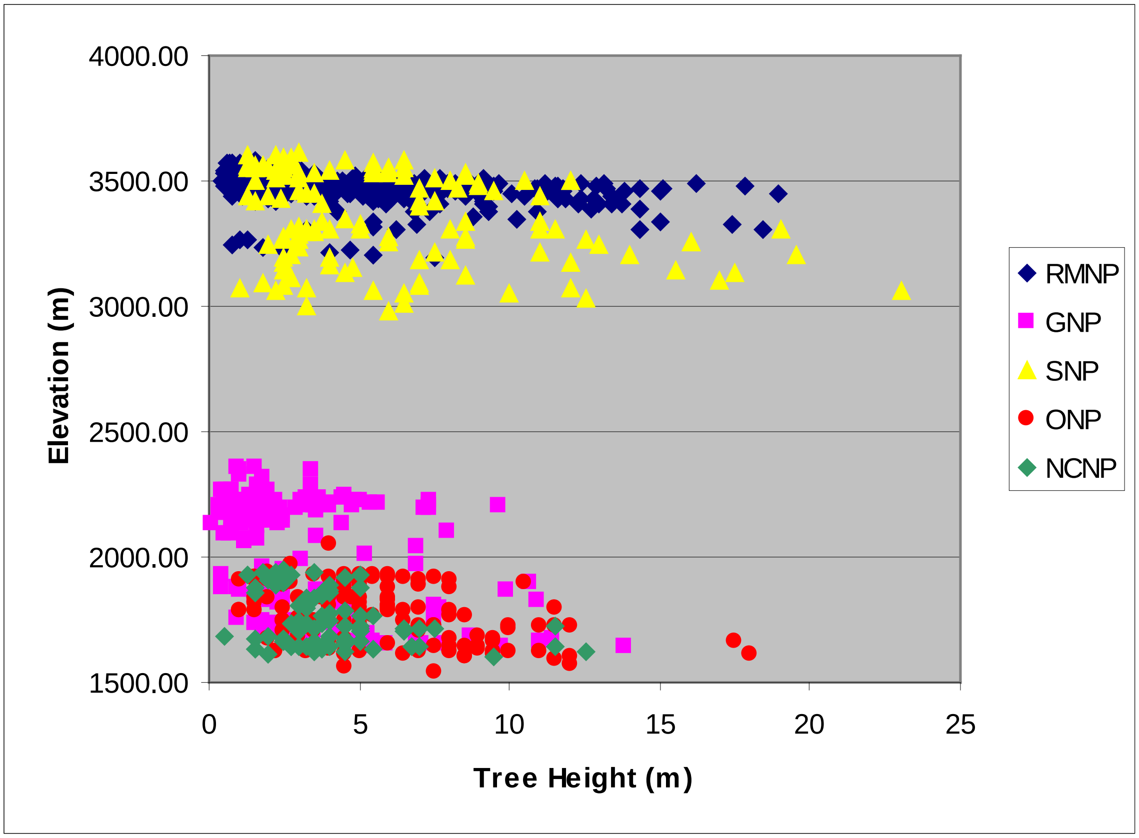


Figure 2.2: Tree height vs. elevation for all field sample points.

Results shown in Table 2.2 quantify (1) the percentage of sampled ATE trees and tree patches that were found adjacent to other treeline vegetation (typically alpine tundra), (2) mean sample point tree height, (3) the percentage of sampled trees and tree patches larger than the 4x4 meter size of Ikonos imagery pixels, (4) the mean slope angle of the sample ATE points from each study area, and (5) the percentages of ATE samples taken from locally concave and convex areas. These field data are useful for (1) showing the general character of treelines in each study area with respect to the setting of the ATE, and (2) by providing a means with which to compare regionally distributed study sites. ATE sample points in all Parks, other than SNP, were located adjacent to other vegetation in a majority of the time, with NCNP and RMNP having particularly high values. Mean tree height values ranged from 3.28 to 6.07 meters, with the tallest ATE trees found in SNP. Tree patch sizes were typically above the 4x4 meter size of Ikonos imagery pixels for all sites except SNP. Together, tree height and patch size results indicate that the ATE samples in SNP typically captured taller, more isolated trees compared to samples from the other study areas. The mean slope angle results show that ATE samples in RMNP were noticeably more gradual than those found in the other study areas. The percentages of concave and convex slope positions indicate that ATE trees in the Pacific Northwest (i.e., ONP and NCNP) heavily favor locally convex areas.

Study Area	Percent Adjacent to Vegetation	Mean Tree Height	Percent Patch Size > 4 Meters	Mean Slope Angle	Percent Concave	Percent Convex
RMNP	93.09%	4.37	91.87%	15.40	36.51%	22.92%
GNP	80.72%	3.28	70.48%	19.19	25.30%	33.73%
SNP	15.91%	6.07	26.52%	18.30	28.17%	37.32%
ONP	77.17%	5.75	87.40%	18.38	11.81%	52.76%
NCNP	98.75%	4.05	93.75%	20.73	0.00%	92.50%

Table 2.2: Summary statistics for ATE sample points within each sample area.

2.5.1 Results - Detailed Case Study in Rocky Mountain National Park

As the study area with the largest sample size, RMNP is well suited for a more detailed analysis of the relationships between ATE characteristics, topographic settings, and imagery products. Given the number of variables available in the field dataset, a number of analyses are possible, but only a few are highlighted here. Tree height structure is related to ATE elevation, but it does not have a simple, linear relationship (Figure 2.3). However, when the data are subdivided by growth form a pattern is evident, with the uppermost ATE samples being almost entirely in the krummholz class, and lower samples being predominately composed of upright trees.

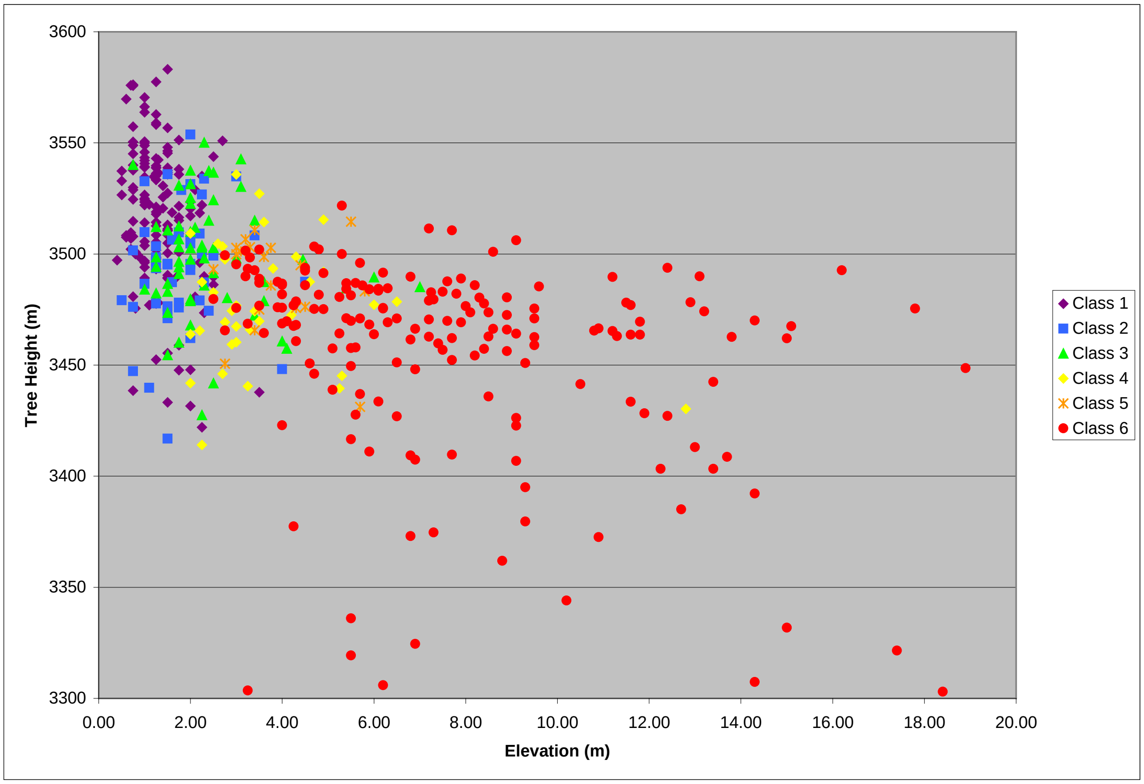


Figure 2.3: The ATE sample point elevation and tree height, color coded according to growth form. The classes range from krummholz (class 1) to upright trees similar to those found in the subalpine forest (class 6). Full descriptions of the classes are provided in section 2.4.1.

The relationship between the Normalized Difference Vegetation Index (NDVI) and Leaf Area Index (LAI) was explored (Figure 2.4) to test the utility of using remotely sensed imagery to approximate a biophysical parameter of ATE vegetation. The results from this analysis show no notable trend between NDVI and LAI for ATE samples, although this relationship may emerge if sites above and below the ATE are included in similar analyses. Additional NDVI datasets were tested (i.e., those derived from Landsat TM and ETM imagery) and trends were similarly absent. Likewise, no trends were found when testing the relationships between tree height and any NDVI values, or tree height and measured LAI. Furthermore, none of these relationships improved when controlling for the effects of elevation, slope aspect, slope angle, slope curvature, patch size, or adjacent landcover (i.e., bare rock or other vegetation).

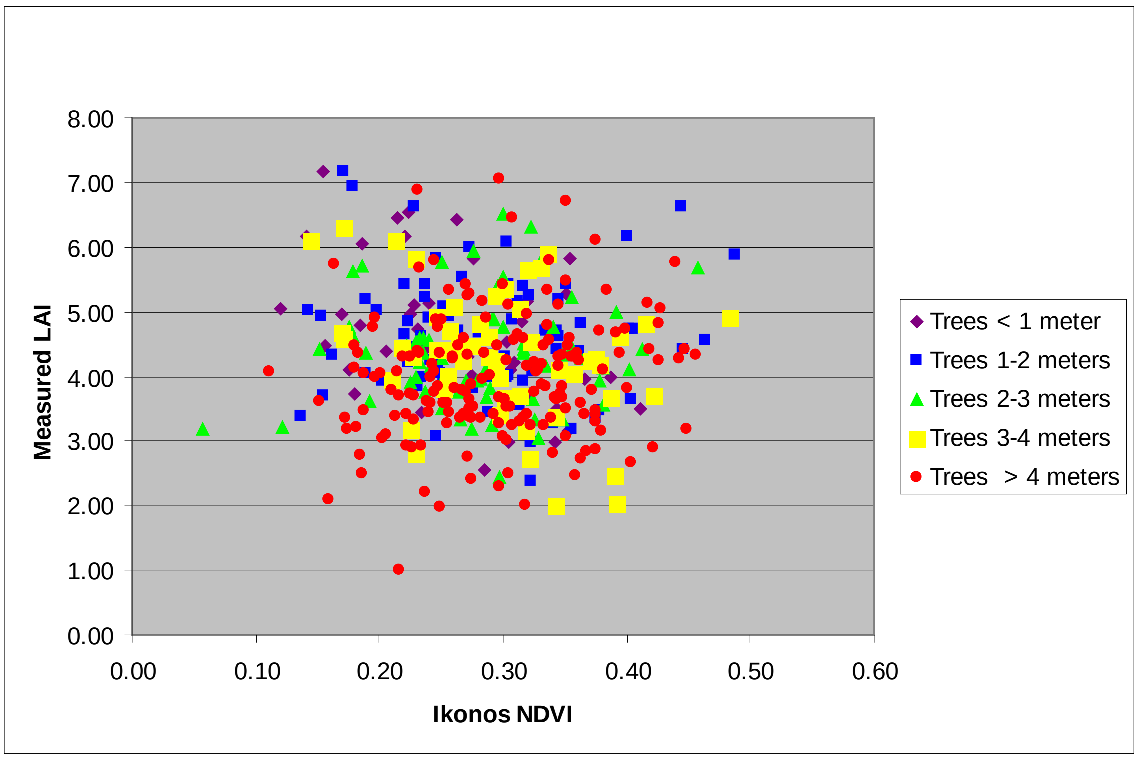


Figure 2.4: The relationship between field measurements of Leaf Area Index (LAI) and the Normalized Difference Vegetation Index (NDVI) derived from 4-meter spatial resolution Ikonos multispectral imagery. Sample points are color coded by tree height class.

Flagging was common in the ATE within RMNP (i.e., 404 of 492 sites had obviously flagged trees). Because flagging occurs in the lee-side of trees, an inverse flagging direction histogram (Figure 2.5) is used to show the prevailing winter wind direction. The dominant direction (n=254) of flagging in RMNP indicates that winds were typically from the west (i.e., 270 +/- 22.5 degrees).

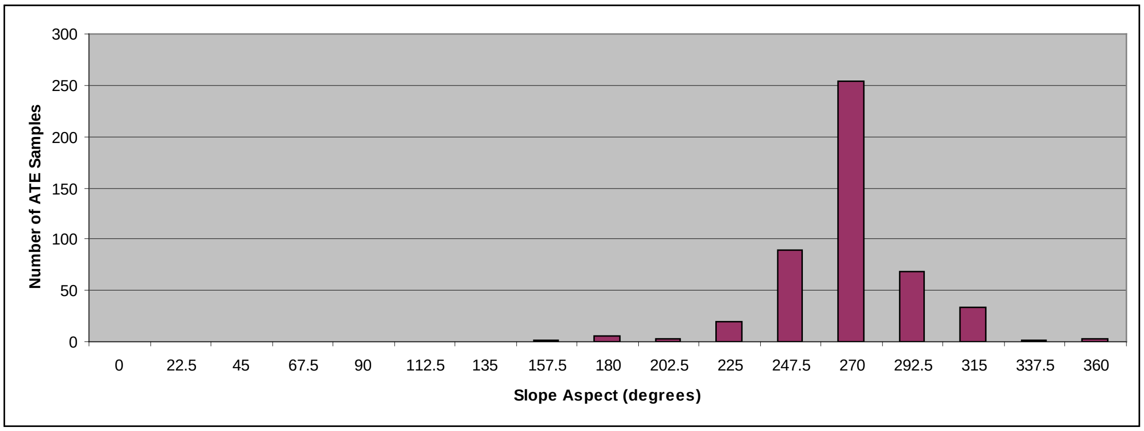


Figure 2.5: Inverse flagging direction (i.e., dominant winter wind direction) distribution for ATE trees in RMNP.

2.5.2 Results - Data Source Comparisons

The final set of results is intended to quantify the relationships between field-based measures of topographic conditions and comparable metrics captured from digital data sources. Relationships between data derived from the different approaches are shown for slope aspect and slope angle in Figures 2.6 and 2.7 respectively. Slope aspect measures generally have a strong, linear relationship. In contrast, the relationship between slope angle measurements, while statistically significant, is surprisingly weak (i.e., $r^2 = 0.1893$). Slope curvature measures (not shown) produced no discernable trend between field based measures and those derived from DEMs.

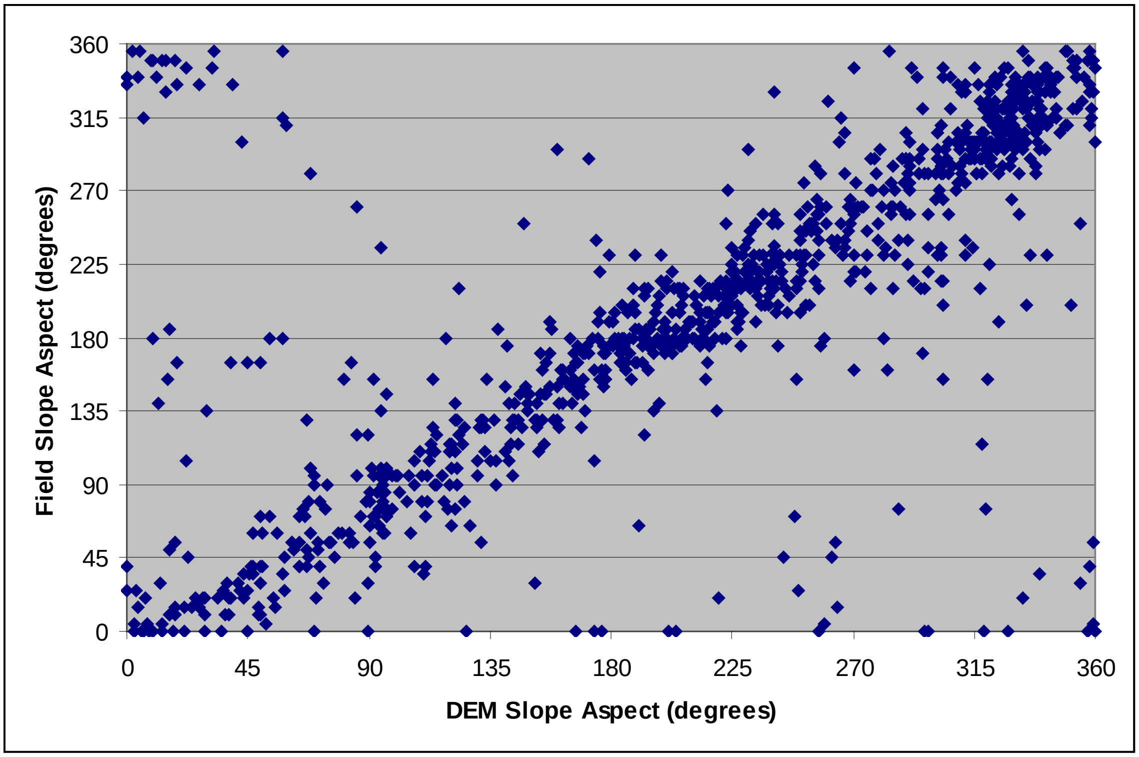


Figure 2.6: The relationship between estimates of slope aspect collected in the field and those derived from DEMs. No r^2 is provided for this graph as 0 and 360 degrees are equivalent.

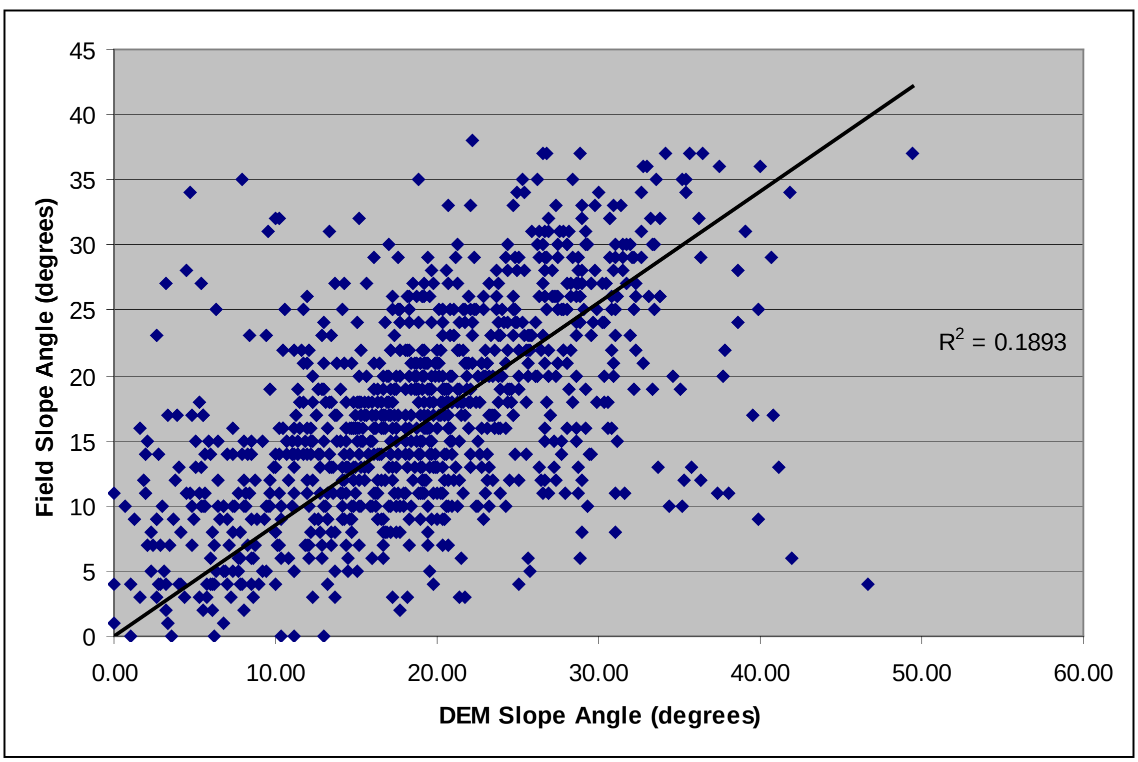


Figure 2.7: The relationship between field estimates of slope angle and those derived from DEMs.

2.6.0 Discussion - Site Comparisons and Regional Context

Variability in ATE elevation at the regional scale is evident in Figure 2.2, as the ATE samples from the southernmost study areas (i.e., RMNP and SNP) have higher ATE elevations than those found in the northern study areas (i.e., GNP, ONP, NCNP). This finding supports the well established relationship between ATE elevation and latitude due to the inverse relationship between latitude and temperature (e.g., Körner 1998a). Among the northern study areas, the lower ATE elevations found in ONP and NCNP support the hypotheses that treelines in the Pacific Northwest are suppressed by (1) the amount and character of snow that falls in this area (i.e., more snow and higher water content of the snow), and (2) the mass elevation effect (i.e., mountains in maritime areas reach temperatures limiting to tree growth at lower elevations than continental mountains due to the increased elevation range relative to the surrounding landscape and/or ocean) (c.f., Holtmeier 2003). These findings are further supported by the percentage of the ATE samples in ONP and NCNP that are in convex locations, likely due to thinner snow packs found in these locations in winter and the resulting easier snow-melt dates. Variability in ATE elevation within the study areas also provides a means of differentiating the study areas. In GNP, for example, there is a wide range in ATE sample point elevations due, in part, to widespread and frequent snow avalanche activity (Walsh et al. 1994) and the commonality of structurally controlled treelines that constrain the ATE well below its climatic limit (c.f., Malanson et al. 2007). In contrast, the variability in ATE elevation in the other parks is proportionally more attributable to intra-Park temperature and precipitation gradients.

The results presented in Table 2.2 inform general trends in the character of the ATE for each study area including (1) the effects of species composition on ATE vegetation patterns, (2) the relationships between properties of sampled ATE trees and local geomorphic history, and (3) the relative proportion of ATE controlling factors (e.g., structural vs. climatic) present within the Parks. The importance of the relationship between species composition, geomorphic history, and ATE character is evident when results from SNP are compared to those from the other study areas. SNP is unique among the study areas because foxtail pine is the most common tree species within the ATE of this Park. Unlike the spruce, fir, and hemlock species inhabiting the ATE in the other study areas, foxtail pine does not readily assume a stunted, krummholz growth form. When foxtail pine is found within the ATE, therefore, it is typically as a tall, isolated, upright tree. The physiological characteristics of foxtail pine help explain the comparatively high mean tree height values and the low percentage of trees and tree patches smaller than 4x4 meters. SNP is also unique among the study areas with respect to the percentage of ATE samples adjacent to vegetation, as there is very little herbaceous vegetation found at high elevations in this study area. The reason for this finding is that, despite providing a stable foundation upon which soils can form, the granitic rocks found in the Sierra Nevada Mountains break down into very granular, nutrient poor soils with poor water retention capacity.

Furthermore, soils in SNP are not supplemented by loess deposition like those found in the other granitic study area (i.e., RMNP).

For all study areas except SNP, the percentage of ATE sample points adjacent to other vegetation types is suggestive of the proportion of the ATE limited by structural controls. This relationship exists because tree samples found next to bare rock are often coincident with sheer cliffs and/or slopes with unstable substrate that is not conducive to the development of soils capable of supporting herbaceous vegetation. When compared to RMNP and NCNP, results show that GNP and ONP have a higher proportion of ATE samples in which trees occur next to bare areas, supporting previous findings that structurally controlled treelines are often found in these Parks (c.f., Malanson et al. 2007). The importance of the Parks' geomorphic history is further indicated by the average slope angle of the ATE sample points. In the case of heavily glaciated Parks like GNP and NCNP, ATE sites tend to occur on steeper slopes. In contrast, Parks with less recent or less severe periods of glaciation, and/or those possessing underlying geology more resistant to glacial scouring, have, on average, more gradually sloping ATE areas. These results are directly related to the geological conditions of the study areas, as rocks coincident with sampled treelines in SNP and RMNP were very stable and resistant to erosion (i.e., they provide a better foundation upon which soils can develop).

2.6.1 Discussion - Detailed Case Study in Rocky Mountain National Park

Results from intra-Park analyses conducted for RMNP show several interesting patterns, most notably the relationship between tree height and ATE elevation, which suggests that there is an upper threshold above which upright trees cannot grow (i.e., approximately 3520 meters). However, no such lower boundary was evident as krummholz trees (class 1) are occasionally found at lower elevations than even upright trees (class 6). This suggests that just as there are topographically advantageous sites found in the upper reaches of the ATE, there are topographically disadvantageous areas found in lower areas. Such topographically disadvantageous areas may include particularly windy areas, recently disturbed areas, and areas that have unusually late lying snow.

The presence (and relative proportion) of flagged trees found within the ATE is important as flagging is an indication of the damage (e.g., needle loss) caused by winter winds, often through abrasion from blowing snow and ice (Tranquillini 1979). Observations from RMNP and GNP show that ATE trees are frequently flagged, thereby indicating that wind has a direct impact on ATE trees in these areas. In contrast, flagging was comparatively rare in SNP, ONP, and NCNP, which supports observations that snow and ice in these Parks are less likely to be transported by winds. If used as parameterization or validation data for wind models in complex terrain, the flagging data collected for this research may also be useful for assessing the spatial locations and patterns of snow drifts occurring within the ATE (Hiemstra et al. 2002). Results from such models are particularly desirable given the ecological importance of snow to the ATE as a source of winter insolation (Tranquillini 1979). Flagging data for RMNP illustrate, not surprisingly, that winds are predominately out of the west. However, these data are not uniform across space and produce interesting, multi-scaled patterns when mapped.

No relationship was found between NDVI and LAI values for the RMNP ATE samples. While disappointing, this result was not entirely surprising, as there were important scale mismatches between the LAI samples (i.e., collected within an area approximately 2x2 meters) and the imagery sources (i.e., 4x4 meter and 30x30 meter pixels for Ikonos and Landsat imagery respectively). Another notable issue was that the LAI samples were taken at the edges of patches, meaning the pixels associated with these data points are likely to contain multiple landcover types (i.e., mixed pixels). Adjacent landcover and patch size data were collected, in part, to be used as additional parameters for assessing the relationship between NDVI and LAI. However, these data proved ineffective for informing results as adjacent vegetation was fairly consistent (i.e., only 34 of 492 sample points had adjacent landcover that that was not at least a majority vegetation) and few sampled tree patches (n=40) were identified as being equal to or smaller than the size of an Ikonos pixel below. Other possible explanations for the poor relationship between NDVI and LAI include (1) the effect of different data collection dates, as the images were acquired four years prior to the field data; and (2) the inappropriate use of the measurement device used to collect LAI, which is designed for use in diffuse lighting conditions such as those found during dusk and dawn.

2.6.2 Discussion - Data Source Comparisons

Comparisons of field-based and DEM-based measures of topographic settings showed mixed results, with measures of slope aspect generally agreeing with each other, measures of slope angle having a significant albeit weak relationship, and measurements of slope curvature having no discernable relationship. Explaining the discrepancy in comparisons between measurement types requires acknowledging shortcomings in the DEM dataset, the methods with which DEM derivates were produced, and important scale differences between seemingly comparable metrics. The data underlying the DEMs are USGS topographic maps originally produced by field surveys and subsequently updated using air photographs. Topographic maps were scanned to create high resolution images, from which the slope contour lines were extracted, and continuous DEMs were produced by interpolating areas between the contour lines. Therefore, the DEMs retain some of the fundamental limitations present in the original survey maps; most notably that, while capturing a tremendous amount of information, DEMs are not detailed enough to capture subtle topographic changes, particularly in complex terrain typical of ATE areas. The ramification of this shortcoming is that DEM derivatives are typically accurate for metrics that vary relatively little at scales of 10s to 100s of meters (e.g., slope aspect). In contrast, slope curvature in mountainous terrain has significant fine scale variability that simply cannot be captured within common 30x30 or 10x10 meter USGS DEMs. In fact, DEM-based slope curvature measures in complex terrain are reflective of the total hillslope curvature, rather than local terrain undulations more pertinent to ATE pattern-process relationship. Further limiting the utility of DEM derivatives for detailed topographic analyses are the methods by which they are produced, which involve computations based on multi-cell windows (e.g., 3x3) that further smooth the resulting metrics. In contrast to the DEM-based measures, the field-based metrics collected for this research capture detail at finer spatial scales (i.e., they capture variability *within* a 10x10 meter area), as they are intended to capture ecologically relevant microtopographic conditions coincident with each ATE sample. Given these issues, the DEM derivatives and the field metrics are effectively incomparable for highly variable topographic metrics like slope curvature.

2.7.0 Conclusion

Field metrics described in this Chapter are (1) illustrative of important pattern-process relationships influencing the ATE across the western U.S., and (2) useful for differentiating study areas with respect to ATE character. The field data by-in-large support previous ATE research findings including (1) the relationships between ATE elevation and latitude; (2) lowered ATE elevations in the Pacific Northwest, likely attributable to the volume and type of snow falling in this area (3) high ATE elevation variability in GNP, likely resulting from a high proportion of structurally controlled treelines and high snow avalanche prevalence; (4) the preferential growth of ATE trees on convex areas in the Pacific Northwest, likely in response to increased snowfall and snow density in this area; (5) the importance of ATE species composition on tree height and patch size, as evident by the comparative uniqueness of SNP, where foxtail pine is the most prominent ATE tree species; (6) the increased occurrence of ATE samples adjacent to bare rock in study areas (i.e., GNP and ONP) that possess a greater proportion of structurally controlled treelines and/or unstable substrate conditions that deter soil formation; and (7) the relationship between ATE elevation, tree height, and growth form in RMNP, where the uppermost trees were almost exclusively krummholz. Unexpected results include (1) the lack of a relationship between field measurements of LAI and NDVI calculated from satellite imagery; and (2) the generally poor relationship between field-based and DEM-based measures of topographic variables, in particular slope curvature. Both of these findings are attributable to important mismatches in the spatial scales of these datasets.

2.8.0 References

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

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

Bader, M. Y., M. Rietkerk, and A. K. Bregt. 2007. Vegetation structure and temperature regimes of tropical alpine treelines. *Arctic Antarctic and Alpine Research* 39: 353-364.

—. 2008. A simple spatial model exploring positive feedbacks at tropical alpine treelines. *Arctic Antarctic and Alpine Research* 40: 269-278.

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

Batllori, E., J. J. Camarero, J. M. Ninot, and E. Gutierrez. 2009. Seedling recruitment, survival and facilitation in alpine Pinus uncinata tree line ecotones. Implications and potential responses to climate warming. *Global Ecology and Biogeography* 18: 460-472.

Bekker, M. F. 2005. Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, U.S.A. *Arctic, Antarctic, and Alpine Research* 37: 97-107.

Brown, D. G. 1994. Predicting vegetation types at treeline using topography and biophysical disturbance variables. *Journal of Vegetation Science* 5: 641-656.

—. 2001. A spectral unmixing approach to leaf area index (LAI) estimation at the alpine treeline ecotone Pages 7 - 21 in A. Millington, Walsh, S.J., and Osborne, P., ed. *GIS and Remote Sensing Applications in Biogeography and Ecology*. Kluwer, Dordrecht.

Brown, D. G., D. M. Cairns, G. P. Malanson, S. J. Walsh, and D. R. Butler. 1994. Remote sensing and GIS techniques for spatial and biophysical analyses of alpine treeline through process and empirical models. Pages 453-481 in W. K. Michener, Stafford, S. and Brunt, J., ed. *Environmental Information Management and Analysis: Ecosystem to Global Scales*. Taylor and Francis, Pennsylvania.

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

Butler, D. R., G. P. Malanson, and D. M. Cairns. 1994. Stability of alpine treeline in Glacier National Park, Montana, U.S.A. . *Phytocoenologia* 22: 485-500.

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

Cairns, D. M. 1999. Multi-scale analysis of soil nutrients at alpine treeline in Glacier National Park, Montana. *Physical Geography* 20: 256-271.

—. 2001. A comparison of methods for predicting vegetation type. *Plant Ecology* 156: 3–18.

Cuevas, J. G. 2000. Tree recruitment at the Nothofagus pumilio alpine timberline in Tierra del Fuego, Chile. *Journal of Ecology* 88: 840-855.

Daniels, L. D., and T. T. Veblen. 2003. Regional and local effects of disturbance and climate on altitudinal treelines in northern Patagonia. *Journal of Vegetation Science* 14: 733-742.

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

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

Holtmeier, F. K. 2003. *Mountain Timberlines: Ecology, Patchiness, and Dynamics*. Springer, Berlin.

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

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

—. 2003. *Alpine Plant Life: Functional Ecology of High Mountain Ecosystems*. Springer-Verlag, Berlin.

Kullman, L. 1996. Recent cooling and recession of Norway spruce (Picea abies (L.) Karst.) in the forest-alpine tundra ecotone of the Swedish Scandes. *Journal of Biogeography* 23: 843-854.

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

Malanson, G. P., D. R. Butler, D. B. Fagre, S. J. Walsh, D. F. Tomback, L. D. Daniels, L. M. Resler, W. K. Smith, D. J. Weiss, D. L. Peterson, A. G. Bunn, C. A. Hiemstra, D. Liptzin, P. S. Bourgeron, Z. Shen, and C. I. Millar. 2007. Alpine treeline of Western North America: Linking organism-to-landscape dynamics. *Physical Geography* 28: 378-396.

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

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

Paulsen, J., U. M. Weber, and C. Korner. 2000. Tree growth near treeline: Abrupt or gradual reduction with altitude? *Arctic Antarctic and Alpine Research* 32: 14-20.

Resler, L. M. 2006. Geomorphic controls of spatial pattern and process at alpine treeline. *Professional Geographer* 58: 124-138.

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

Scuderi, L. A., C. B. Schaaf, K. U. Orth, and L. E. Band. 1993. Alpine treeline growth variability: Simulation using an ecosystem process model. *Arctic and Alpine Research* 25: 175 - 182.

Tranquillini, W. 1979. *Physiological Ecology of the Alpine Timberline: Tree Existance at High Altitudes with Special Reference to the European Alps*. Springer-Verlag, Berlin.

Walsh, S. J., D. R. Butler, T. R. Allen, and G. P. Malanson. 1994. Influence of snow patterns and snow avalanches on the alpine treeline ecotone. *Journal of Vegetation Science* 5: 657-672.

Walsh, S. J., A. Moody, T. R. Allen, and D. G. Brown. 1997. Scale-dependence of NDVI and its relationship to mountainous terrain. Pages 27-55 in D. A. Quattrochi, and Goodchild, M.F., ed. *Scaling in Remote Sensing and GIS*. CRC/Lewis, Boca Raton, FL.

Wilson, J. B., A. D. Q. Agnew, and M. T. Skyes. 1993. A vegetation switch as the cause of a forest/mire ecotone in New Zealand. *Journal of Vegetation Science* 4: 273-278.

Chapter 3

SCALE-DEPENDENT RELATIONSHIPS AMONG ALPINE TREELINE ELEVATION AND ABIOTIC VARIABLES HYPOTHESIZED TO CONTROL THE ECOTONE

3.1.0 Introduction

The Alpine Treeline Ecotone (ATE) is defined as the boundary zone between closed-canopy subalpine forests and the highest individual trees or tree patches found upslope. In areas without major anthropogenic disturbances the ATE is principally a temperature boundary above which trees cannot tolerate one or more aspect(s) of the harsh alpine climate. Research dating back over 200 years has consistently affirmed the relationship between alpine treeline elevation and air temperature at regional-to-global scales (Holtmeier 2003). The relationship between the ATE and climatic conditions has led to great public and scientific interest in the ATE as a potential bellwether of global climate change. However, an explanation of treeline as a climatic boundary, although accurate in a simplistic sense, masks the complex set of interacting environmental controls acting upon the ATE that vary greatly across space and scale.

ATE research has traditionally been conducted at local or global scales, with much less research devoted to exploring (1) how environmental conditions influence the ATE at intermediate scales, and (2) how relationships between ATE characteristics and abiotic controls vary with scale. Fine scale (i.e., from the scale of the hillslope to several mountains in close proximity) treeline research is typified by numerous studies that identify important ATE controls within specific study areas. Environmental variables identified as important for ATE dynamics within such fine scale studies include geomorphic controls (e.g., Butler et al. 2004), micro-topographic effects (e.g., Resler et al. 2005), sky exposure (e.g., Germino et al. 2002), herbivory (e.g., Cairns and Moen 2004), soil fertility (e.g., Malanson et al. 2002), and moisture conditions (e.g., Bunn et al. 2005a). Coarse scale studies (i.e., regional-to-global scale analyses), in contrast, consistently associate treeline position with some aspect of air or soil temperature (e.g., Körner 1998b).

The environmental controls affecting the ATE are geographically variable and act at varying spatial and temporal scales to produce conditions. For example, when micro- and meso-topographic controls are combined with regional climatic gradients, each treeline can be considered a unique ecotone with respect to how it is produced and maintained by the environment. The intent of this research is to systematically test the scale-dependencies inherent to hypothesized ATE controls across the western United States by applying a standard analytical framework to an array of sites distributed throughout the region. The set of hypothesized controls are drawn primarily from Holtmeier (2003), Körner (2003), Seastedt et al. (2004), Billings (1973, 1979), and Tranquillini (1979). The set of hypothesized controls used in this research is not exhaustive as datasets detailing all controls identified as important in previous research were not available for one or more study sites. This work may be viewed as an empirical test of the hypothesized scaled controls on alpine treeline formulated by Holtmeier and Broll (2005).

3.2.0 Background

Findings from ATE research conducted at regional-to-global scales suggest that treeline elevation correlates strongly with air temperature (e.g., between 5 and 7.5 degrees Celsius (Körner 1998a)). In contrast, research examining treelines at finer spatial scales often describes variations in treeline elevation associated with site specific environmental and ecological conditions. The differences between environmental conditions affecting the ATE at local and regional scales are typically explained by fine scale ATE controls that act to modify the overlying climatic gradients (Körner 2003). Numerous local-scale factors have been identified as important controls on the ATE including (1) differential radiation loading associated with slope and aspect (Baker and Weisberg 1995), (2) topographic roughness that produces sheltering effects from wind and promotes snow drift development (Hiemstra et al. 2002), (3) feedback effects from existing trees in the ecotone including solar insulation (Germino et al. 2002), (4) pedogenesis (Malanson et al. 2002), (4) geomorphic or geologic controls (Resler et al. 2005), and (5) disturbances such as forest fires or spatially reoccurring snow avalanches (Walsh et al. 1994). These and other fine scale ATE controls are highly variable across space in response to both coarse scale climatic gradients and site specific differences such as geologic conditions and history.

Geographic variations ultimately determine the relative importance, and in some cases even the direction of influence, of environmental conditions affecting the ATE. Complicating the relationship between climatic conditions and ATE controls are issues such as lagged effects related to the slow rate of change within the ATE (Baker and Weisberg 1997), interactions (i.e., feedbacks) between ATE controls that may magnify or diminish pattern-process relations (Malanson 1997, Wilson and Agnew 1992), differing ATE tree species compositions that do not respond uniformly to ATE controls (Holtmeier 2003), and changes in the relative importance of ATE controls in response to specific life stage limitations of trees (i.e., limitations of a seedling often differ from limitations for a mature tree) (Germino et al. 2002, Smith et al. 2003).

Although numerous local-scale ATE controls have been identified, the actual mechanisms by which the trees are kept from advancing to elevations above the ATE are still somewhat contentious. Körner (2003) discusses five prominent hypotheses for how low temperatures control the ATE trees including: (1) by causing frost damage, (2) by contributing to winter desiccation, (3) by causing reproduction limitations, (4) by producing negative carbon balances, and (5) by inhibiting resource utilization. Of these hypotheses, most support has been found for the resource utilization hypothesis (Körner 2003), however, all of the hypotheses may retain validity under certain circumstances and/or in specific geographic locations.

An alternative hypothesis is presented by Germino et al. (2002) and Smith et al. (2003) that, in contrast to Körner's list, focuses mainly on conditions regulating seedling establishment. Findings from this research suggest that, once established, trees are quite capable of long term survival within the ATE. Furthermore, Germino et al. (2002) and Smith et al. (2003) found that seedling survival is closely associated with sky exposure due to photoinhibition caused by the combination of (1) chilling effects at night and (2) rapid heating shortly after sunrise. Under this hypothesis, air temperature is still the driving force behind treeline control, but diurnal temperature extremes and the presence or absence of sheltering vegetation and/or topographic features are the critical variables for explaining seedling survival and mortality.

Whatever underlying mechanisms are responsible for controlling trees within the ATE, coarse scale abiotic variables within the environment, such as climatic conditions, provide the template for these mechanisms and are, therefore, considered higher-level ATE controls. Such an understanding was proposed by Billings (1979) and was extended by Seastedt et al. (2004). Scale is a fundamental property of these theoretical frameworks, which rely on a hierarchical set of controls. This structure is effectively an application of hierarchy theory (Allen and Starr 1982), whereby controls operating at the coarsest scales (i.e., the globe or the region) ultimately bound the possible states of the system at lower scales. This structure is recursive in nature, as each successively finer scale control will be bounded from above and constrain levels below. With respect to the ATE, this framework implies that climatic conditions establish a standard ATE elevation for each treeline site, while finer scale controls can potentially increase or decrease ATE elevation by modifying micro-climatic conditions within the limits imposed from above.

3.3.0 Study Area

The study area for this research consists of 26 ATE sites distributed throughout the western United States (Figure 3.1). The sites are divided into primary and secondary sites based upon the intensity of sampling and the presence of ground-control data. In other words, primary sites have accompanying field data and additional samples. The five primary sites include Glacier National Park, Montana; Rocky Mountain National Park, Colorado; Sequoia/Kings Canyon National Park, California; Olympic National Park, Washington; and North Cascades National Park, Washington. Field data were collected for this research at these primary sites, which also have a rich history of ATE research upon which to draw. The 21 secondary sites are distributed throughout the region to provide a more complete sample of ATE. The full set of 26 sites provides a rich and varied set of ATE sites for analysis, including dramatically different precipitation regimes (e.g., coastal mountains compared to continental ranges), incident radiation (i.e., sites span over 13 degrees of latitude), and geologic conditions (e.g., volcanic domes, granitic ranges, and crumbling sedimentary peaks).

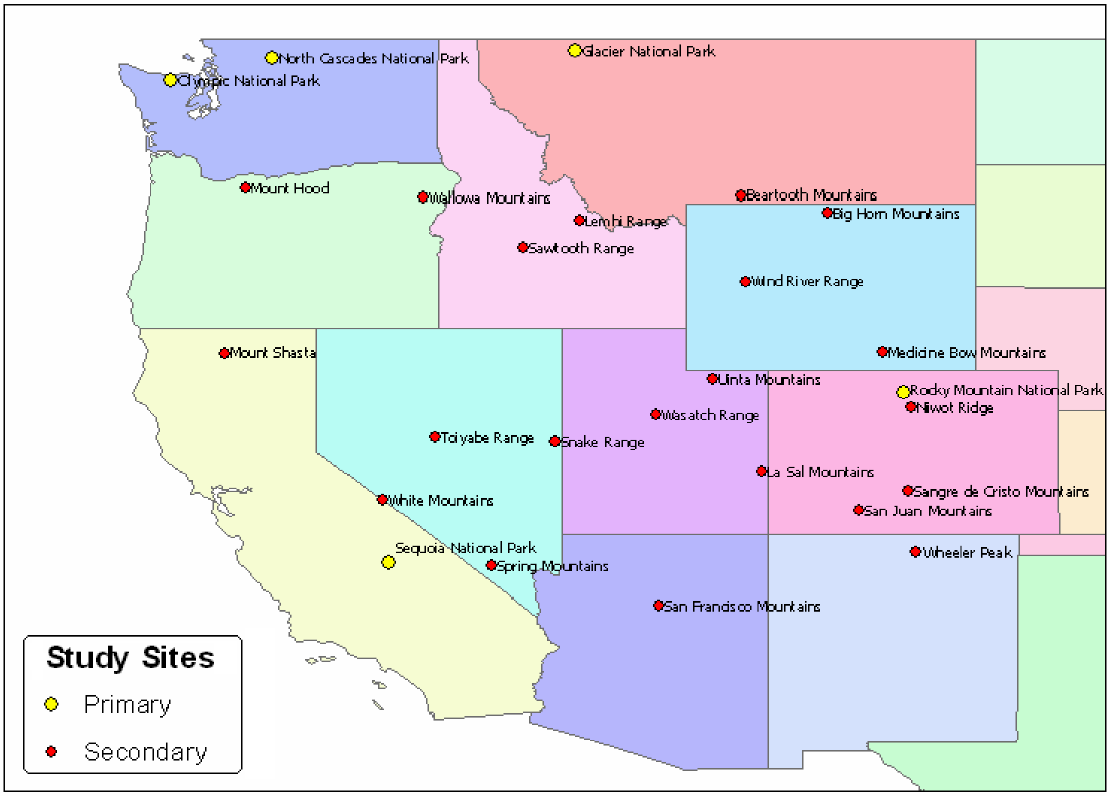


Figure 3.1: Study sites map. Primary sites were more extensively sampled and have associated validation data acquired in the field. Secondary sites were sampled only from satellite imagery, with validation done using higher spatial resolution air photos.

3.4.0 Research Overview

The research question explored by this project is “How do hypothesized environmental controls on the elevation of the alpine treeline ecotone vary with scale across the western U.S.?” The theoretical basis for this research is provided by the work of Billings (1973, 1979), Seastedt et al. (2004), and, in particular, Holtmeier and Broll (2005) (Figure 3.2). These authors describe hierarchical sets of controlling variables, acting at different scales, that combine to produce localized ATE characteristics. The basic intent of this research is to perform an empirical test of these hypotheses by exploring the scale-dependencies of relationships between ATE elevation and a set of environmental variables, for sites distributed across the western United States. This research is unique because it synthesizes data collected from many geographically distinct study sites and compares these ATE samples using a single, systematic methodological approach. The research goal is to bridge some of the gaps between ATE assessments at global scales and those focused on local scale, site specific ATE research, typically conducted using different methodologies.

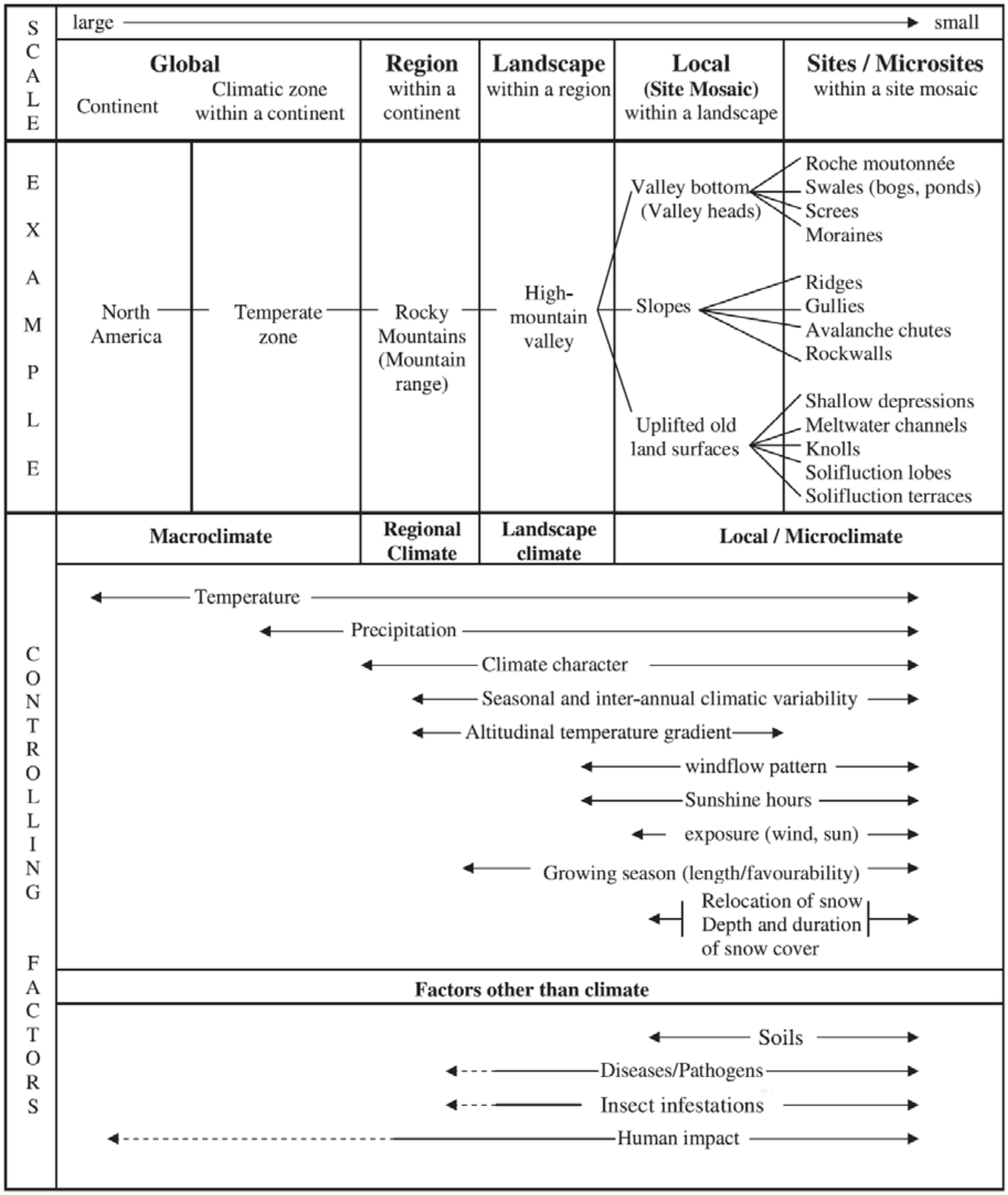


Figure 3.2: Treeline controlling factors and their hypothesized scale of influence (Holtmeier and Broll 2005).

The underlying ecological hypothesis guiding this research is that air and/or soil temperatures, and associated variables such as incident solar radiation or growing degree days, are the dominant controls on treeline elevation at the scale of the region. Because this research is based in a mid-latitude region, the relationship between ATE elevation and temperature in the western U.S. is expected to be nearly linear, with warmer temperatures leading to higher treelines (Körner 1998b). The strength of the relationship between ATE elevation and temperature will diminish at finer spatial scales as temperature controls are modified by localized characteristics (e.g., topographic shading that decreases incident solar radiation).

The relationship between ATE elevation and precipitation is hypothesized to be another major regional control on the ATE. The bulk of annual precipitation in the ATE of the western United States falls as snow and, while rain provides a source of summer moisture, snow is more important as a control on ATE characteristics due to features beyond the provision of moisture. Snow benefits trees within the ATE by insulating them from abrasive blowing snow and the coldest winter temperatures, both of which contribute to the death of exposed needles through desiccation (Tranquillini 1979). However, snow may also limit trees in the ATE when it lasts late into the spring or summer, thereby shortening the growing season (Rochefort and Peterson 1996) and encouraging the growth of pathogens such as the snow fungus Herpotrichia. Within the context of this research, precipitation is hypothesized to be an important control at the scale of the region, but the relationship between precipitation and ATE elevation is considerably more complex than the relationship between ATE elevation and temperature because of the dramatic differences in the volume and character of precipitation that falls at the selected ATE study sites. In fact, annual precipitation volume is so variable that the relationship between it and ATE elevation can be considered beneficial (i.e., leading to higher ATE elevation) in dry areas such as the southern Rocky Mountains, or detrimental in moist areas like the Olympic Mountains. Precipitation is also a powerful ATE control at intermediate scales due to rain shadow effects common to most mountain ranges. Like air temperature, precipitation interacts with and is modified by topography at fine spatial scales. For example, snow may accumulate in depressions and sheltered areas as it is scoured from exposed sites and redeposited in the lee of hillslope features such as boulders and/or shelters produced by tree patches (Hiemstra et al. 2002).

ATE tree species composition is another hypothesized regional scale control on ATE elevation, as trees have different life strategies for overcoming the harsh climate present within the ATE (Young and León 2007). For example, ATE areas in the Rocky Mountains are typically dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), which commonly grow in dense krummholz mats that improve micro-site conditions for the trees through positive feedbacks. Krummholz mats are a viable option for these species because they can survive despite the death of the apical meristem (i.e., if the main stem (trunk) dies, the trees can remain alive and continue to send out horizontal branches capable of turning upright and becoming the new dominant stem) (Smith et al. 2003). These spruce-fir krummholz mats are capable of persisting for centuries as both species are capable of vegetative reproduction, whereby they sprout new roots from low-lying, partially buried branches, to create a cloned tree. This life strategy is particularly useful in the ATE where "good" years for seedling establishment are rare and vegetative reproduction may be necessary to ensure continued presence of trees within the ecotone.

In contrast to the Rocky Mountains, the ATE in the southern Sierra Nevada Mountains is dominated by foxtail pine (*Pinus balfouriana*), a single stemmed tree that does not commonly form krummholz mats and cannot reproduce vegetatively. These seemingly disadvantageous traits are mitigated, in large part, by the extremely long lifespan of these pines, which effectively ensures a stable presence in the ATE in the absence of disturbance. In addition to producing a contrast in the vegetation patterns of the ATE, tree species composition may influence ATE elevation as treelines with similar species compositions are likely to have similar ATE elevations even after controlling for other environmental influences that are coincident with changes in species ranges.

At spatial scales ranging from micro-sites to the scales of 50-100 km (i.e., the approximate size range of the primary study sites used in this research), topographic controls including slope aspect, slope angle, slope curvature, sheltering effects from wind and/or solar radiation, and topographic moisture potential significantly modify ATE conditions related to the coarser scale climatic gradients. These topographic variables are hypothesized to surpass climatic conditions in their relative importance as controls upon ATE characteristics at intermediate-to-fine spatial scale (e.g., individual hillslopes), where differences between climatic gradients are slight. Interpreting topographic influences is complex because they modify coarser scale conditions that are geographically variable. Interactions between topographic conditions and treeline, therefore, are best studied at individual study sites where the overlying conditions are relatively constant. As a regional scale analysis, this research is not designed to capture the intricacies of topo-climatic interactions, but it will identify the scales at which topographic variables emerge as significant ATE controls.

3.5.0 Methods

Statistical analysis is the central methodological approach used in this project. Treeline elevation samples from all study sites comprise the dependent variable, while the independent variables are environmental variables associated with each sample that approximate hypothesized ATE controls identified in prominent ATE literature by Billings (1973, 1979), Holtmeier (2003), Holtmeier and Broll (2005), Körner (1998b) Körner (2003), Richardson and Friedland (2007), Seastedt et al. (2004), and Stevens and Fox (1991). The data for this research were collected from a combination of satellite images, air photos, and spatial data sets including Digital Elevation Models (DEMs); and from existing modeled climate data produced using the DAYMET model (http://www.daymet.org/) developed by the University of Montana, Numerical Terradynamic Simulation Group. These data sources were selected because they are consistent across all study sites, which enables a single, systematic analytical approach appropriate for quantitative analysis of treeline ecotones across the region. However, important drawbacks of using these data sets include non-uniform spatial resolutions among the independent variables, coarse spatial resolution relative to the scale of the of many hypothesized ATE controls, and hypothesized ATE controls for which no data are available. These limitations are unavoidable trade-offs of requiring a consistent set of metrics for a large number of study sites distributed across a geographically diverse region.

The analysis presented in this chapter simultaneously explores ATE character at both coarse and fine scales and, therefore, it is necessary to specify the nature of elevation within this research, as elevation has been used as both a dependent and independent variable within previous alpine treeline research. The distinction between using elevation as a response or predictor variable is often made using the spatial scale of the analysis. Coarse scale analyses (i.e. regional to global) typically treat treeline elevation as a dependent variable because elevation is associated with climatic factors such as the relationship between latitude and temperature. In contrast, treeline research conducted at finer scales often uses elevation as an effective surrogate for localized temperature due to the inverse relationship between these factors that results from processes including (1) adiabatic cooling of rising air, (2) limited land surface area available in high mountains for absorbing solar radiation and radiating that energy as sensible heat, and (3) reduced atmospheric insolation.

Fundamental factors underlying this research that are relevant for determining the use of elevation include (1) temperature is identified as the dominant control on treeline position; (2) local temperatures are directly related to coarse scale climatic processes that define the elevation at which one or more aspect(s) of temperature limit or prohibit tree growth; (3) localized temperatures respond relatively uniformly along an elevational gradient, thereby linking fine scale temperatures to regional conditions and making the local relationship between elevation and tree presence or absence relatively static (i.e., without additional local mediating influences treeline elevation would occur at an essentially uniform elevation); and (4) the variability in the position of treeline elevation at fine scales results from topographic influences and feedback processes that mediate regional scale climatic conditions to produce microclimatic settings amenable for supporting trees (or not). Given these factors, treeline elevation was selected as a dependent variable for this analysis as it responds to both regional climatic controls and localized topographic influences, thereby effectively capturing the combined effect of multiple factors across a range of spatial scales.

3.5.1 Sampling Design

The fundamental sampling unit for this research is the belt transect that is oriented perpendicular to the ATE. Each ATE transect extends approximately 50 meters upslope from the highest identifiable tree and 50 meters downslope from the estimated edge of the closed-canopy forest. The procedure for deriving the treeline sample sites is adapted from Baker and Weisberg (1995), who manually derived cross sectional, belt transect samples of alpine and subalpine vegetation in Rocky Mountain National Park, Colorado using air photos.

As in Baker and Weisberg (1995), sampling for this research required manual transect creation using a head-up digitizing approach, but several image processing steps were utilized before transects creation in an effort to generate random sample locations appropriate for statistical analysis. The first step was a simple classification of Landsat TM or ETM images for each study site to create tree/no-tree surfaces. In these classifications, pixels identified as trees were given a numerical value of 1 while other landcover types were coded as a zero. Pixel values were then summed within a 5x5 pixel moving window, and resulting values between 10 and 15 (i.e., 40-60% tree covered) were extracted to form a new image. The new image contained only a small fraction of the pixels from the original image, as most areas are either almost completely tree covered or without trees. Random points were generated within the new image that served as the seed points for the belt transect samples. By-in-large, this approach was effective for isolating the ATE in its various states (i.e., ranging from crisp boundaries to wide ecotones dominated by patchy vegetation). However, a few non-ATE edges were captured, including lower treelines (e.g., the forest-prairie ecotone), lake shores, and areas where human activity had created landcover edges. Any random sample point that fell within non-ATE areas was deleted during the transect digitization process. A total of 1006 samples (i.e., belt-transects) were digitized for the 26 study sites. Study sites had unequal numbers of samples, with a higher sampling density in primary sites than in secondary sites. Differences in sample sizes are attributable to (1) variability in the size of the study sites and (2) limited amounts of treeline available to sample, which was particularly problematic in some of the secondary sites.

3.5.2 Sample Dimensions

The size of the belt-transects was an important consideration for this research. Transects extended 50 meters beyond the estimated boundaries of the ATE because (1) distinguishing the edge of an ecotone is an arbitrary endeavor and this buffer provided a margin of error; (2) a primary hypothesis of this research is that the ATE is affected by micro-site conditions, and these conditions don't necessarily end abruptly at the location of the highest tree; and (3) this approach limited the amount of non-ATE area in each transect. Determining an appropriate belt-transect width was another challenge as ATE samples that are too narrow capture local peculiarities rather than the overall characteristics of the hillslopes on which the ATEs were found. In contrast, belt-transects that are too wide may merge multiple ATE types and blur the relationships between ATE elevations and the environmental controls most responsible for producing them. Pattern metrics were used to empirically determine the appropriate width of the belt transects. Landcover pattern was used because any dramatic shift in the pattern of the ATE may imply a different underlying set of controls (e.g., compact ecotones in structurally-controlled areas compared to wide ecotones in climatically-controlled areas with gradual slopes). As such, a transect width that captures an ATE sample of a consistent pattern is more likely to contain a section of the ecotone influenced by similar controls. The procedure for determining the appropriate belt transect width involved (1) classifying high spatial resolution satellite imagery for the five primary study sites into a basic classification scheme, (2) creating belt transects of various widths from a subset of the digitized ATE transects, (3) deriving pattern metrics for the classified landcover within each belt transect, and (4) graphing the relationship between transect width and the selected pattern metric to empirically determine the approximate width at which patterns stabilized (Figure 3.3). Ikonos imagery was selected for this analysis because it captures fine-scale heterogeneity while limiting mixed pixels, and because it has a similar spatial resolution to the air photos, from which the ATE samples were digitized. Prior to classification the Ikonos images were georectified (RMSE < 0.5 pixels), and topographic illumination corrections were performed to minimize the effects of aspect-related incident radiation differences. The topographic illumination correction approach selected for this research was a modified version of the C-correction that was described by Riaño et al. (2003). The landcover classification method consisted of an unsupervised classification approach, with the class attribution based upon panchromatic air photos and ground-truth data collected from each primary study site. The landcover classes consisted of conifer trees, herbaceous vegetation (e.g., deciduous shrubs and trees in riparian areas and on avalanche paths), tundra and meadow, bare rock, snow and ice, and water and shadow classes. Accuracy assessments were done for all classifications and the results were all in excess of 73% (kappa > 0.56) (Table 3.1).

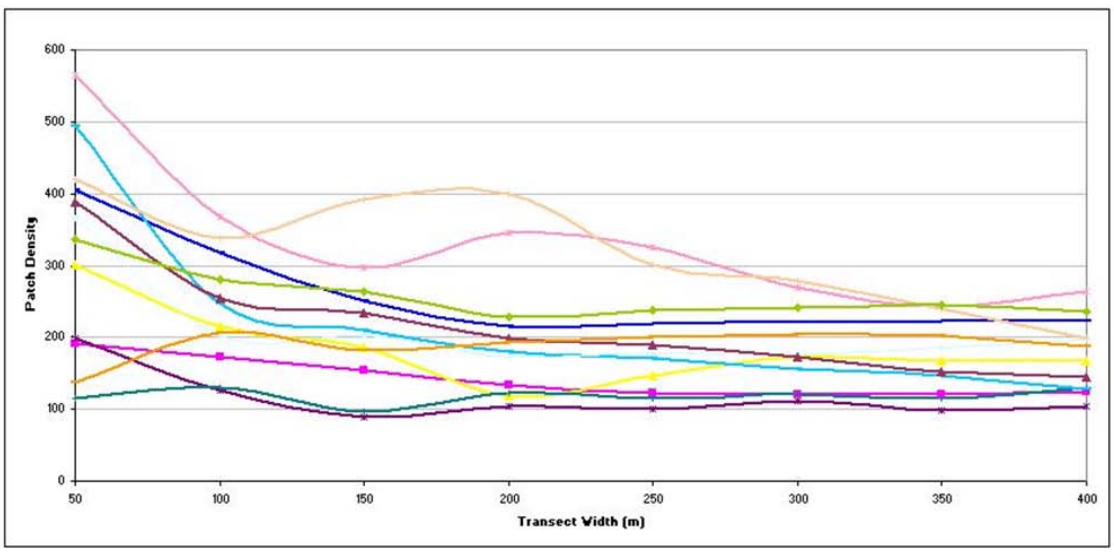


Figure 3.3: The appropriate width of the belt-transect ATE samples was derived using the scale at which the pattern metric (patch density) stabilized (300 meters).

Site	Overall Accuracy	Kappa
Glacier National Park	91%	0.86
Rocky Mountain National Park	91%	0.86
Sequoia National Park	92%	0.89
Olympic National Park	93%	0.87
North Cascades National Park	88%	0.82
San Francisco Mountains	95%	0.89
Mount Shasta	82%	0.72
White Mountains	87%	0.79
Niwot Ridge	92%	0.87
Sangre de Cristo Mountains	90%	0.86
San Juan Mountains	90%	0.85
Lemhi Mountains	92%	0.88
Sawtooth Range	88%	0.83
Beartooth Mountains	93%	0.91
Snake Range	78%	0.65
Spring Mountains	73%	0.56
Toiyabe Range	90%	0.85
Wheeler Peak	90%	0.83
Mount Hood	90%	0.84
Wallowa Mountains	80%	0.71
La Sal Mountains	83%	0.75
Uinta Mountains	87%	0.81
Wasatch Range	77%	0.65
Bighorn Mountains	83%	0.74
Medicine Bow Mountains	90%	0.85
Wind River Range	85%	0.79

Table 3.1 Accuracy assessment results for landcover classifications performed for each study area.

3.5.3 Variable Creation and Extraction

Independent and dependent variables for each sample were extracted from spatial datasets acquired for each study site. To maintain consistency, all sites used identical datasets and processing steps. Treeline elevation, the dependent variable in this analysis, was defined as the highest identifiable tree in the ATE within the manually digitized transect. The elevation values were extracted directly from digital elevation models. This approach was selected because it produced an unambiguous estimate of ATE elevation that was consistent for all study sites, despite differences in tree species and their survival strategies (e.g., upright growth compared to krummholz). However, in some cases the highest tree in the ecotone is effectively an outlier that does not necessarily share many of the controls that limit the ecotone characteristics in the sample transect (e.g., a tree perched on a high ledge above an otherwise structurally-controlled treeline). An alternative dependent variable, therefore, was also generated for each transect by extracting the elevation for the transect midpoint, which was influenced by the estimates of upper and lower ATE boundaries. The ATE elevations within the set of 1006 samples range from 1282 meters in Olympic National Park to 3767 meters near Wheeler Peak, NM.

Calculating the independent variables was considerably more complicated, due in large part to the number of variables used. These independent variables were divided into four categories: DEM derivatives, modeled climate data, species compositional data, and geographic distance. Since the belt-transect was used as the unit of analysis, summary statistics (e.g., mean, standard deviation, and range) were derived for each dependent variable, and they constitute the variables actually used in the statistical analyses.

In this research both climatic and topographic data rely on the summary statistics (i.e., mean and standard deviation) for capturing the state of the variables. However, a notable distinction between the climatic and topographic variables is necessary as the simple summary statistics used for analyses captured fundamentally different information. In the case of the topographic data, the mean values capture the general *spatial* conditions at each ATE sample, while standard deviation measures quantify the *spatial* variability in the local topographic setting. The summary statistics for climatic data, in contrast, capture *temporal* variability, as the mean and standard deviation values capture trends and variability at single locations over time. Mixing datasets that capture spatial and temporal variability does not, however, preclude these datasets from being used in the same analysis as it can be argued that the topographic variables effectively create micro-climatic spatial patterns. By including both topographic and climatic data summaries, therefore, the spatial and temporal variability in the climatic conditions hypothesized to control the ATE can be included within a single analytical framework.

3.5.4 Topographic Variables

DEM derivatives comprise a set of hypothesized environmental controls including belt-transect elevation range, slope aspect, slope angle, topographic moisture, and slope curvature. All DEMs used in this analysis were 10-meter resolution datasets. These DEMs were fairly coarse data from which to derive detailed topographic information important for ATE species, but they represent the best data available for all study sites.

Belt transect elevation range is simply the difference between the highest and lowest points in the belt transect. This variable is relevant for ATE research because it is indicative of the basic type of ecotone control limiting trees in each belt transect. For example, in climatically-controlled ATE samples the belt transect elevation range is likely to be high, as tree patches extend far upslope from the edge of the closed canopy forest. In contrast, orographic-treelines (e.g., sheer cliffs that preclude tree establishment) are likely to have low belt transect elevation ranges, as these ecotones are relatively compact. For treelines characterized by disturbances, in particular those experiencing recurring, topographically influenced snow avalanches, belt transect elevation range will be relatively high.

Slope aspect is an important ATE control that influences the amount of solar radiation incident on a slope, which is further associated with soil moisture conditions due, in part, to the drying effects of higher air temperatures. Slope aspect also influences moisture conditions through interactions with wind and the resulting redistribution of snow. In the western United States, the prevailing west winds often lead to snow removal from exposed, west-facing slopes and ridges, and snow deposition on east-facing slopes and in sheltered areas (Hiemstra et al. 2002). Solar radiation and wind exposure combine to form a moisture gradient that is generally southwest (driest) to northeast (wettest) as southwest facing slopes receive direct solar radiation in the afternoon, which typically is the warmest part of the day, and experience snow scouring from winter winds.

Slope aspect measurements were generated on a per-cell basis from the DEMs. Cosine aspect and sine aspect surfaces were derived to capture the north-south and east-west relationships, respectively. An additional transform

(Equation 3.1) was calculated to more effectively capture the SW-NE moisture gradient that arises from, respectively, exposure to and shading from intense afternoon sun (Beers et al. 1966). In the resulting transformed aspect surface grid cell values range from -1 (southwest-facing) to 1 (northeast-facing). Cells from the resulting grids that were within each belt transect sample were summarized on a per-transect basis to produce the independent variable used in the analysis.

$$\text{Transformed Aspect} = \text{cosine}(\text{aspect} - 45^\circ)$$

Equation 3.1: Transformed aspect is designed to provide a gradient from the warmest slopes (southwest facing) to the coolest slopes (northeast facing) in topographically complex environments in the northern hemisphere.

Slope angle is a measure of the steepness of the landscape. Slope angle is directly relevant to the ATE because steep slopes typically (1) lack establishment sites for tree seedlings, (2) limit or preclude pedogenesis, (3) experience frequent mass-movements and/or may be covered by the resulting colluvium, (4) drain rapidly leading to less available moisture for plants, and (5) affect solar radiation incident on land surfaces. Slope angle is indirectly relevant for the ATE because it is associated with topographic sheltering that may encourage ATE tree establishment and growth, or produce late-lying snow patches that preclude trees.

Mean slope angle values were calculated for each belt transect to serve as an independent variable in this analysis. Efforts were also made to capture micro-topographic effects from the DEMs by calculating topographic roughness (Riley et al. 1999), a measure of topographic texture. This variable was intended to address the significant role micro topography plays in tree establishment in the ATE (Resler et al. 2005). Unfortunately, the estimate of surface roughness was limited by the level of spatial detail available in the DEM and the resulting variable was strongly correlated with slope angle.

Slope curvature is a measure useful for characterizing the overall slope shape. Slope curvature is relevant for the ATE because concave slopes encourage winter snow accumulation, while convex slopes are more exposed and encourage snow removal by wind. As previously mentioned, different snow volumes affect soil moisture and growing season length in the ATE. Plan, profile, and total curvature were calculated following Moore et al. (1991). The resulting curvature grids were coded to represent flat areas as a zero, convex areas as positive values, and concave areas as negative values. The magnitude of the raster cell values indicates the degree of local concavity or convexity within the eight adjacent cells (i.e., using a 3x3 window).

Soil moisture conditions are produced through a combination of the amount and timing of precipitation, temperature, vegetation cover, soil characteristics, and slope conditions. Relative soil moisture conditions, however, can be estimated using moisture drainage patterns that are based solely on topographic data. For this research a relative moisture metric, Topographic Wetness Index (TWI) (Equation 3.2), was used to estimate topographic moisture potential (Beven and Kirkby 1979). TWI is useful for defining a drainage network and is relevant for ATE research because (1) it can identify how likely a stream channel is to be located within each belt transect, and (2) streams are often coincident with snow avalanche paths. Snow avalanche paths are considered an orographic ATE control (Holtmeier 2003) as these disturbances tend to reoccur only in valleys with conditions found upslope that are conducive for the excessive snow accumulation. TWI may also be used as an estimate of soil moisture for generalizing conditions within the belt transects and, therefore, for differentiating relatively wet and dry slopes. For example, trees growing in ATE sites that are potentially limited by too much moisture, such as those in the Pacific Northwest, might benefit from drier, well drained sites. In contrast, trees growing at drier sites, like those found in the southern Rocky Mountains may experience higher growth rates, lower mortality, and/or easier establishment conditions on topographically moist slopes.

$$\mathrm{TWI} = \ln(a/\tan\beta)$$

Equation 3.2: TWI estimates the local soil moisture for each grid cell based within a DEM. In this equation *a* is the upslope area and *B* is the local slope for each cell.

3.5.5 Climatic Variables

Climatic data utilized within this Chapter consist of DAYMET data produced by the University of Montana, Numerical Terradynamic Simulation Group. These data are products of the MTCLIM model (Hungerford et al. 1989), which incorporates meteorological base station data and topographic datasets to generate spatially-contiguous meteorological estimates in a raster format. The DAYMET data archive is available online as an 18-year dataset that ranges from 1982 to 1997 and has a spatial resolution of 1-km. Data are available for each 1-km cell, with a daily temporal resolution, and for the entire nation, presented as maps of the climatic variables summarized on an annual temporal basis. DAYMET data included in this research are annual averages and standard deviations for air temperature, precipitation, incident Short Wave RADiation (SWRAD), Growing Degree Days (GDD), and Frost Degree Days (FDD). Within the framework of this analysis it is important to note that these climatic variables are only used for analyses conducted at coarse spatial scales (i.e., greater than 200 km) as climatic variables are not independent at finer scales. This is not a concern at coarse scales, however, because the density of meteorological base stations is sufficient to ensure that modeled climate data for areas hundreds of kilometers apart are not based upon identical weather station input data.

With the exception of the precipitation data, all the collected measures represent temperature related phenomena. These datasets were each tested to determine which was most strongly associated with ATE elevation. Somewhat counter intuitively, air temperature, and to a lesser extent GDD and FDD, were not expected to be strongly associated with ATE elevation because (1) the temperature thresholds for trees in the ATE areas are similar for sites around the world (Körner 1998b) and (2) the sampling design for this research only captures sites that contain ATE, as opposed to including sites above and below the ecotone. In selecting a variable that can accurately represent temperature effects it is useful to remember (1) that, generally speaking, temperatures are cooler in higher latitudes, and (2) that air masses are lifted and cooled adiabatically as they cross mountains. The critical temperature thresholds relevant for tree establishment and growth, therefore, will be reached at lower elevations in higher latitude mountains. As such, the variable representing temperature within this research framework must be able to incorporate the effects of heating at a scale that exceeds adiabatic processes. Of the available variables, SWRAD is the most appropriate proxy for temperature as it captures the amount of incident energy, which is primarily a function of latitude and cloud cover, and is more indicative of the broad spatial trends that affect the elevation at which ATE air temperature thresholds are reached. For reference, mean annual temperatures for the sample transects range from -5.37 to 5.76 degrees Celsius in the San Francisco Mountains and the Olympic Mountains respectively. With respect to SWRAD, the opposite relationship is evident, as sites in the Pacific Northwest have low average annual incident radiation compared to sites in the Desert Southwest.

DAYMET data, while representing the best available source for modeled shortwave radiation and precipitation estimates for the western U.S., also introduce several shortcomings to this analysis. Key examples include: (1) an 18-year data range that may be too short to capture important climatic trends; (2) coarse spatial resolution data that cannot capture important micro-climatic effects; (3) important effects related to timing of meteorological events (e.g., the date of snow melt) that are obscured by the annual averaging; (4) annual data that do not differentiate between types of precipitation, which is important because snow has functionality in the ATE beyond providing moisture; (5) an annual time-step based on calendar dates that is not especially relevant to seasonality at the study sites; (6) DAYMET data that are least accurate for remote areas far from weather stations, including many sites comprising the study areas for this research; and (7) analyzing the relationship between ATE elevation and DAYMET data at fine scales is impossible because elevation is a key input for this climate model. DAYMET data are used, despite these shortcomings, because they capture broad climatic trends which, if the hypothesized ATE control structure is correct, are the scales most relevant for climatic data. The apparent resolution mismatch between 1-km climate data and variables derived from 10-meter DEMs is also of limited importance for this research because the DEM derivatives are aggregated to produce measurements at the scale of the belt transect, which is at least 100x300 meters in size. Finally, annually averaged data are used instead of more temporally detailed data because of (1) the large number of samples collected and (2) the intent to maintain a single, consistent set of dependent variables.

3.5.6 Species Composition

The species compositional data used for this research consisted of range maps for trees and shrubs created by Little (1971) and digitized by the USGS. Trees and shrubs are used rather than tundra or meadow plants because detailed range maps are rare or non-existent for such species and characteristics of these small plants cannot be easily distinguished from remotely sensed imagery. In general, all conifers common to the ATE were available in the Little (1971) dataset, as were many species of deciduous trees and shrubs. However, Little's range maps (1971) did not include all relevant species, with willows being particularly poorly represented in the dataset. As a result, the species dataset is less complete than was hoped, but it represents the best available source of spatial tree species data at the scale of the region.

A total of 17 tree and shrub species were selected for inclusion in this analysis. Although many other tree species were present in areas adjacent to the ATE sites, most do not grow within the ecotone. The list of ATE species (Table 3.2) was derived from a combination of a literature review and field observations. Of these species, none were found at all 26 study sites.

Common Name	Latin Name
Subalpine fir	*Abies lasiocarpa*
Rocky Mountain maple	*Acer glabrum*
Green alder (i.e., slide alder)	*Alnus sinuata* (including *A. viridis* and *A. crispa*)
Mountain alder	*Alnus tenuifolia* (including *A. incana* and *A. rugosa*)
Yellow cedar	*Chamaecyparis nootkatensis*
Common juniper	*Juniperus communis*
Creeping juniper	*Juniperus horizontalis*
Rocky Mountain Juniper	*Juniperus scopulorum*
Subalpine larch	*Larix lyallii*
Engelmann spruce	*Picea engelmannii*
Whitebark pine	*Pinus albicaulis*
Rocky Mountain bristlecone pine *	*Pinus aristata*
Foxtail pine	*Pinus balfouriana*
Lodgepole pine	*Pinus contorta*
Limber pine	*Pinus flexilis*
Quaking aspen	*Populus tremuloides*
Douglas fir	*Pseudotsuga menziesii*
Mountain hemlock	*Tsuga mertensiana*
Geyer's willow **	*Salix geyeriana*
Western mountain ash	*Sorbus scopulina*
Sitka mountain ash	*Sorbus sitchensis*

Table 3.2: Tree and shrub species included in the ATE species composition analysis.

* Little (1971) does not distinguish the Rocky Mountain bristlecone pine (*Pinus aristata*) from the Great Basin bristlecone pine (*Pinus longaeva*).

** Numerous species of willow are common to the ATE, particularly in the Rocky Mountains, but few species were available from range maps. Geyer's willow was selected because it was the species most attributable to the ATE available within this dataset.

As with the climatic data, there were notable limitations to the tree species range maps, most importantly the spatial scale of these data. To mitigate the coarse resolution of the data, a buffer was applied to the species' ranges to include as many species as possible (i.e., err in the direction of more compositional similarity between sample sites). Several buffer sizes were tested, but ultimately a 5-km buffer was selected because it most closely approximates the estimated error provided in the limited available meta-data accompanying the datasets (USGS 1999). Each belt transect ATE sample was attributed using the buffered range map polygons to create a presence/absence matrix for all samples and all species. The Bray-Curtis dissimilarity calculation was then applied to this dataset. The result was a matrix comparing all belt transects whereby sample pairs with similar species composition had lower values than sample pairs with less similar composition. In extreme cases, a Brey-Curtis dissimilarity value of zero indicates identical species composition, and a value of 1 indicates no species overlap.

3.5.7 Geographic Distance

The final independent variable utilized in this analysis was geographic distance between all pairs of belt transects. Since the basic research question pertains to the spatial scales at which controls are correlated, it was necessary to quantify all distances between all pairs of belt transects. The original datasets for this research were in many different projections and, therefore, all the data were converted to zone-appropriate UTM coordinates for the majority of the processing. However, for calculating geographic distances an alternative approach was required as data points were scattered across four different UTM zones (i.e., 10, 11, 12, and 13). To accomplish the calculation, all belt-transect center points were converted to latitude and longitude (i.e., WGS 1984) and great circle distances were calculated between all possible combinations of points. The resulting distances between the sample points range from 0.2 to 1,968 km.

3.5.8 Statistical Analysis

The statistical approach used in this research is a modified version of the Mantel test (Legendre and Fortin 1989, Mantel 1967). A Mantel test is a type of regression analysis in which the dependent and independent variables consist of the differences between values for each sample point and all other sample points in a data set. This framework facilitates incorporation of multiple types of independent variables in a single analysis, including abiotic characteristics derived from DEMs, ecological variables such as species compositional dissimilarity, and geographic distances between sample points. For this research compositional dissimilarity and great circle distance are already correctly formatted as they are distance matrices. The environmental variables, in contrast, required conversion into distance matrices by calculating the simple difference for each variable between all possible pairs of sample points (e.g., the difference in estimated ATE elevation).

The fundamental statistical procedure underlying Mantel's tests is Pearson's product moment correlation, and the Mantel-r values produced are similar to conventional r values. There are, however, a few key differences between Mantel-r and traditional r values. First, the independent and dependent variables are distances (e.g., the change in ATE elevation and the change in slope aspect) and, therefore, the correlation coefficients do not reflect relationships between these variables directly, but rather the relationship between how these variables change. Second, each sample point is used repeatedly to generate the distance matrices and, therefore, the assumption of independence of the error terms of the samples is violated. As a result, the significance test for a Mantel test cannot be calculated using parametric approaches and, consequently, this parameter is commonly derived using label permutation (Legendre and Legandre 1998). The label permutation approach is conceptually similar to Monte Carlo or bootstrapping techniques, whereby the strength of the actual relationship between the variables is compared to the relationships of thousands of randomly re-ordered combinations of the same data (i.e., the independent variables stay the same while the dependent variable is re-ordered). The resulting p-value is calculated as the percentage of occurrences in which the randomly re-ordered data produce a stronger correlation than the correlation between the actual data, as determined by calculating t-values for each permutation.

The types of Mantel tests used in this research consist of simple and partial Mantel tests. In a simple Mantel test each independent variable is correlated with ATE elevation. Partial Mantel tests use a regression framework that incorporates multiple independent variables, and the relationship actually tested is the correlation between the dependent variable and a single independent variable, after the influence from all other independent variables is removed. This process effectively controls for the influences of other independent variables, and since geographic distance is an independent variable, a partial Mantel regression approach directly incorporates geographic space, thereby controlling for the effects of spatial autocorrelation.

This research also takes the conventional Mantel test one step further in that it tests scale-dependencies in the relationships between the dependent and independent variables. This approach involves analyzing subsets of the full dataset formed after dividing the data into distance classes. The relationships between the dependent and independent variables are then calculated at each scale of analysis. The processing procedure for this consists of unfolding all the distance matrices into vectors and arranging them in a single data table so that each row contains all distance values for a single pair of samples, and each column contains a single dependent or independent variable. Within this format, the data are sorted according to geographic distance. Simple and partial Mantel tests are then done for increasingly small subsets of the samples by effectively deleting the samples that had the coarsest geographic distances. To test the effects of scale, tests were conducted at 25 unique spatial scales. For example, the initial test included all 505,515 sample pairs, and each successive test dropped approximately 40,000 sample pairs (i.e., those that were the farthest apart). The resulting Mantel r and p values from each test were recorded along with the mean geographic distance of the remaining samples. These values were graphed to assess how the relationships between ATE elevation and hypothesized environmental controls vary with scale. Such graphs are advantageous over more commonly used graphs that explore spatial structure in environmental data (e.g., semivariograms) because they show how relationships between two or more variables change with scale, as opposed to examining only spatial variability in individual variables.

A major caveat of the statistical framework is the impact of collinearity, which is often a consideration when dealing with environmental variables. Simple correlation matrices comparing all dependent variables (both original and after being converted into distance matrices) indicated that there were several groups of variables with collinearity. These groups most frequently included variables with the same root data source, such as different measures of slope curvature (e.g., mean plan curvature and mean total curvature). In these cases, the variable with the strongest simple correlation with ATE elevation was selected for inclusion in the statistical analysis, while the other collinear variables were omitted. When no variable was deemed superior to the others in the collinear group (i.e., none were significantly stronger than the others) the most widely used and/or ecologically interpretable variable was selected. The alternative case occurred when a cluster of collinear variables formed from different data sets. One example was slope aspect and a DEM-based calculation of average solar radiation that was not included in this analysis. Variables within all collinear groups were further analyzed by calculating the Variance Inflation Factor (VIF) for each variable. These results were used to delete any remaining problematic variables from the analysis if they exceeded the VIF threshold of 10 suggested by Hair et al. (2006). This threshold is higher than those suggested elsewhere and was selected so as not to lose important variables hypothesized to affect the ATE. The rationale for keeping variables with some degree of collinearity is that the partial regression framework is effective for assessing the relationship between the independent and dependent variable after the covariance between the collinear variables is controlled.

Like all analyses based on correlation, this research does not explicitly link the hypothesized controls to treeline elevation in a causal way, but correlation provides an indication of control and serves as a starting point for models that can more directly address causes and controls of treeline. This research may also be viewed as an empirical test of the hypothesized controls identified by Holtmeier and Broll (2005), because it explicitly focuses on geographic scale within the analysis. Although the environmental variables used in this research do not exactly match those that were hypothesized by Holtmeier and Broll (2005), the concept being tested (i.e., scale-dependencies in relationships between ATE characteristics and environmental conditions) is fundamentally the same.

3.6.0 Results

The final set of independent variables used in the analysis, after trimming the set to reduce the influence of collinearity, consisted of geographic distance, mean annual incident short-wave radiation, mean annual precipitation, belt transect elevation range, maximum TWI, annual precipitation standard deviation, mean total slope curvature, mean slope angle, mean (cosine) slope aspect, and

Bray-Curtis species compositional dissimilarity. Since the Mantel test framework cannot indicate the direction of correlation, a table of simple correlation is included for reference (Table 3.3). Note that Table 3.3 does not show species compositional dissimilarity because this variable is formed by comparing two samples. The results from the statistical analysis utilizing Mantel tests consisted of large data tables that are summarized in Figures 3.4, 3.5, and 3.6. Each data point in the figures represents the Mantel r value for the defined (i.e., color coded) variable at that geographic scale. Significant relationships are indicated by points on the graph, and no Mantel r results were plotted for results with a p-value more than 0.05. Trend lines are used to link significant results to create a more interpretable graph. Gaps in the trend lines indicate non-significant results for the independent variables at those scales. The geographic scale values are the mean geographic distance for all sample pairs used in the associated test. For comparison, corresponding graphs were also generated using the maximum geographic distances for each scale (not shown). The shapes of the curves in the comparison graphs were nearly identical, but each scale value (i.e., the X-axis) was increased by about 50 %.

Environmental Variable	Correlation Coefficient
Mean Annual Shortwave Radiation	0.901878872
Mean Annual Precipitation	-0.734911769
Elevation Range	-0.470631058
Maximum TWI	-0.120393148
Annual Precipitation Standard Deviation	-0.632644865
Mean Total Slope Curvature	-0.03181802
Mean Slope Angle	-0.355448789
Mean Cosine Slope Aspect	0.022901673

Table 3.3: Simple correlation results for between each independent variable and ATE elevation for all sample sites. Note that because all sample points are included some correlation results may be misleading since the relationships between independent variables and ATE elevation vary with space and may even switch between positive to negative relationships.

Figure 3.4 shows simple Mantel test results for each dependent variable vs. ATE elevation for all spatial scales coarser than a single study area. As expected, mean annual shortwave radiation is the variable most strongly correlated with ATE elevation at coarse scales, but this relationship diminishes with increasing spatial resolution. This trend mirrors geographic distance, which indicates a pronounced regional trend in the correlation between ATE elevation and hypothesized environmental controls. Like shortwave radiation, mean annual precipitation and precipitation variability are strongly related to ATE elevation at the regional scale and gradually decline at finer scales. However, the precipitation variables surpass shortwave radiation at fine scales (i.e., < 400 km), a fact that is likely related to orographic precipitation effects present in rain-shadows from nearby mountain ranges also included in this analysis. In contrast to the climatic variables, the topographic variables have weaker relationships with treeline elevation at all spatial scales. The topographic variables are still statistically significant, however, and tend to become stronger at finer spatial scales. The topographic variable most strongly correlated with change in ATE elevation is elevation range, which, as previously mentioned, is included in the analysis because it helps distinguish structurally-controlled treelines from those that are climatically-controlled.

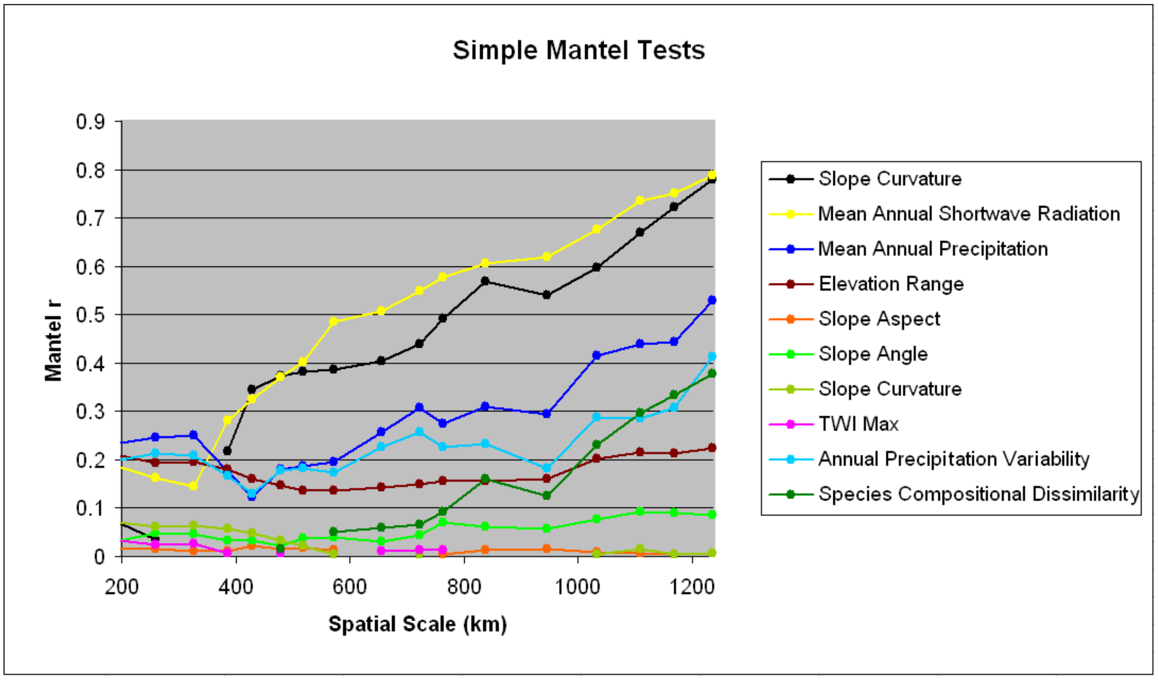


Figure 3.4: Scaled simple Mantel test results that assess the scaled relationship between ATE elevation and each independent variable down to the scale of individual study areas.

Figures 3.5 shows partial Mantel test results for each independent variable vs. ATE elevation at scales greater than 200 km, after controlling for all other independent variables, including geographic space. The trends in this graph are largely the same as those produced by the simple Mantel tests, but the strengths of the relationships are reduced as a result of controlling for the effects of other variables (i.e., collinearity). The continued presence of geographic distance as a significant variable can be interpreted as an effect of spatially varying environmental variables important for controlling ATE elevation that are not included in the analysis. Likely missing variables include geologic condition, geomorphologic history, past disturbances such as forest fires, and climatic effects not adequately accounted for by the variables used in this analysis (e.g., the timing of climatic events such as the first snowfall). As in the simple Mantel test results, the reemergence of significant values for mean annual precipitation at scales of less than 400 km is a feature in the partial Mantel results, a finding that reinforces the hypothesis that precipitation is responding to rain shadow effects at sub-regional spatial scales.

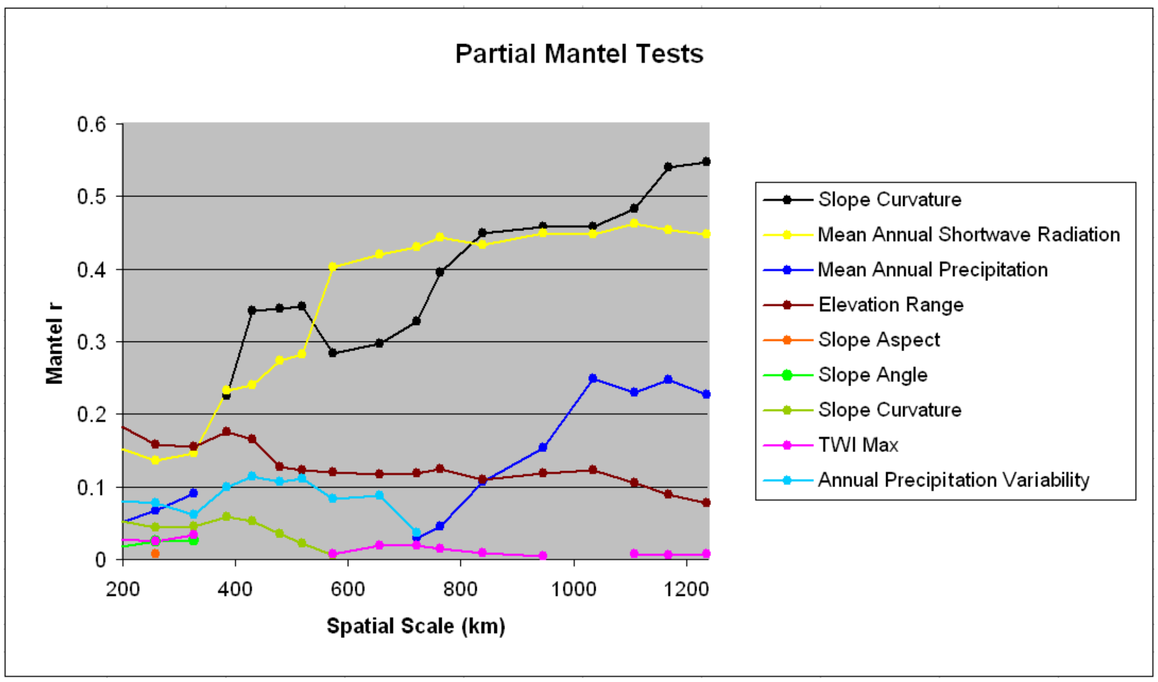


Figure 3.5: Partial Mantel test results that assess the scale-dependent relationship between ATE elevation and each independent variable, after controlling for all other independent variables. Note that gaps in the trend lines indicate spatial scales at which the variables become statistically non-significant.

With respect to compositional dissimilarity, the simple Mantel test results (Figure 3.4) show that species compositional change has a significant relationship with treeline elevation change (i.e., sites with similar composition have similar ATE elevation and vice versa). However, results from the partial Mantel tests (Figure 3.5) do not support this finding. More in-depth analysis of the partial Mantel results indicates that when geographic distance is controlled for, the relationship between species composition and ATE elevation change becomes non-significant. These results do not support the hypothesis that species composition is an important controlling factor for treeline elevation when analyzed at regional scales. However, this finding may merely reflect the collinear relationship between species composition and geographic distance.

Unlike climatic variables that are not independent at intra-study area scales, topographic variables can be analyzed for the full range of geographic distances available in the dataset. Partial Mantel test results for the relationship between ATE elevation and topographic variables, after controlling for the effects of other variables and geographic distance, are shown in Figure 3.6. Unlike Figures 3.4 and 3.5, Figure 3.6 uses a log scale for the x-axis to highlight fine scale relationships. Topographic variables generally had stronger partial correlations with ATE elevation at finer scales. However, slope angle became non-significant at scales below approximately 3 km, suggesting that there may be interaction effects between some topographic variables. In contrast, TWI is only statistically significant within the Mantel test framework at the finest spatial scale. Unlike the climatic variables described above, there are no major shifts from regional to sub-regional controls evident in the topographic variables. This finding was not unexpected as topographic effects are most relevant at regional scales with respect to how they interact with climatic variables.

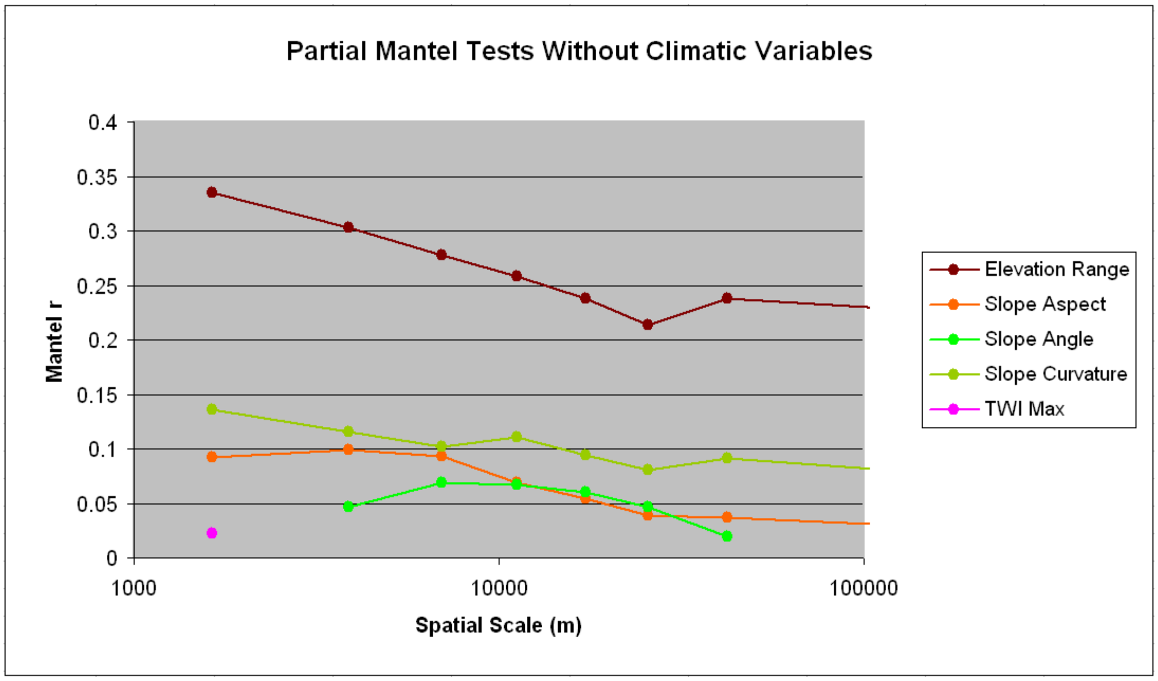


Figure 3.6: Scaled partial Mantel test results that assess the (log) scaled relationship between ATE elevation and each topographic variable, after controlling for all other topographic variables and geographic distance. Note that gaps in the trend lines indicate spatial scales at which the variables become statistically non-significant.

3.7.0 Discussion

This research was, in many ways, a story of making compromises necessary to explore the geographic nature of ATE controls in a new and ambitious way. Despite challenges related to the environmental dataset limitations, results from this Chapter offer new insights into the scale-dependent structure and relative influence of several abiotic variables hypothesized to control the ATE in a mid-latitude region. More importantly, the results from this research are the first to assess ATE controls across a region, at multiple spatial scales, using a consistent, quantitative analytical framework. The utility of these results lies in their ability to (1) help link local studies of ATE controls with studies conducted elsewhere in the region, and by (2) providing an empirical basis for scaling fine scale analyses up, thereby facilitating localized interpretations within a regional-scale context.

Important findings from this research include: (1) supporting the basic hypotheses that regional controls are largely climatic, but climatic variables are inadequate for explaining ATE elevation variability at fine spatial scales, (2) suggesting that precipitation is important on several spatial scales as both regional climatic gradients and localized rain-shadow effects appear to influence ATE elevation, (3) isolating an apparent shift from regional to sub-regional controls at spatial scales around 300-400 km, (4) indicating that an important component of the variability in ATE elevation remains unexplained using the variables included in this model, and (5) findings that do not support the hypothesis that species compositional differences are associated with ATE elevation change.

The first two findings support previous ATE research conclusions, but also explicitly address how the relationships between abiotic variables and ATE elevation vary with spatial scale. Quantifying these relationships is useful because doing so can help define the x-axis (i.e., the spatial scale) associated with the hypothetical ATE control framework depicted in figure 3.2 (Holtmeier and Broll 2005). Furthermore, the first two findings go beyond defining the scales at which abiotic variables are significant (or not), and show the relative importance of the variables with respect to each other. This information fits directly into a hierarchical understanding of ATE controls and may be useful for parameterizing spatially-explicit ATE models designed to predict future states of the ecotone under varying environmental change and/or management scenarios.

The third finding is notable because it suggests that future research at spatial scales above a threshold of 300-400 km should not ignore regional climatic trends. ATE analyses focused on scales below this threshold, however, may be able to treat regional climatic trends as static, or nearly so. This information is also useful for comparing results from analyses conducted at distant sites, as sites farther apart than the identified threshold will require more careful consideration of regional climatic trends. Despite these findings, more analysis is required to further isolate the spatial thresholds significant for influencing ATE character, as the apparent shift occurring at 300-400 km may simply be a product of a switch from inter- to intra-study-area scales of analysis.

The fourth finding suggests that some important variables are missing or inadequately captured by the datasets, sampling design, or analytical approach utilized by this research. Important missing datasets include categorical data such as geologic condition and soil information, datasets that incorporate feedback effects produced by adjacent vegetation types, and data detailing historic conditions at the ATE (e.g., climate and disturbance) that continue to affect present day ATE character. The lack of historical data is largely due to the difficulty of accurately estimating past conditions, particularly over large geographic areas. A related challenge emerges when trying to assess a dynamic ecotone using a dependent variable (i.e., ATE elevation) taken from a single point in time, thereby treating ATE elevation as temporally static. This issue is problematic because the sampling strategy employed in this research does not capture active ATE migration, which is directly related to underlying abiotic controls. Unfortunately, there are no available datasets that capture details pertaining to ATE motion at spatial scales applicable to this research. Results from this research, however, may contribute to the creation of such a dataset through their incorporation into mechanistic ATE models.

Limitations of the datasets actually used for this analysis were a necessary byproduct of requiring identical datasets for constructing a single analysis. Specific data shortcomings include the coarse spatial and temporal resolution of the climate data, the inability to use the climatic data for fine scale analysis due to elevation being an input for the DAYMET model, and the coarse spatial resolution of the DEMs relative to important micro-topographic features. These limitations are particularly problematic at fine spatial scales, where the datasets lack the level of detail to capture subtle environmental features or conditions influencing ATE characteristics. Issues resulting from the coarse scale of the input datasets are evident in Figures 3.4 though 3.6, whereby multiple controls are significant, but none are strongly correlated with ATE elevation at fine spatial scales.

The fourth important finding does not diminish the value of this research as the statistical model was never expected to explain all the variability in ATE elevation. Despite not including all variables hypothesized to influence ATE elevation, the analytical framework and base datasets developed for this research project establish a starting point for future research. Furthermore, the foundational effort demonstrated by this research is useful because new and/or improved datasets can easily be incorporated, as they become available, while the analytical approach can remain unchanged. In this way the level of spatial and temporal detail can be increased for specific datasets without the need to generate new datasets for other variables and/or to devise a new analytical framework. Desirable improvements to the abiotic datasets include modeled climate data with improved spatial and temporal resolution, and topographic variables generated from higher spatial resolution DEMs (e.g., those produced from Light Detection And Ranging sensors (LIDAR)).

The fifth important finding (i.e., a non-significant relationship between ATE elevation and tree species composition) fits with the global understanding of ATE dynamics that attributes ATE elevation, regardless of the species present, to localized temperatures. However, research results by Bader et al. (2007) indicate that species composition does affect ATE responses to abiotic controls at multiple, geographically distant sites in the tropics. These authors attribute the importance of species composition, with respect to ATE controls, to limited available genera in the Hawaiian Islands. In the western U.S., however, such limitations are less apparent as all sites possess species within at least one common ATE genera (i.e., A*bies, Pica, Pinus*).

3.8.0 Conclusion

The results of this research generally support current hypotheses about the scaled relationships between ATE controls and treeline elevation that were proposed by Holtmeier and Broll (2005) and others. Mean annual shortwave radiation is strongly associated with ATE elevation at regional scales, but this relationship diminishes at fine spatial scales. Precipitation is most strongly related to ATE elevation at coarse spatial scales; although there is a notable second peak in this relationship at finer scales that is attributable to rain shadow effects. Differences among topographic variables, although statistically significant, are generally poor predictors of ATE elevation changes, particularly at coarse spatial scales. A likely explanation for the poor relationship between ATE elevation and the topographic variables is that the spatial resolution of the topographic variables is too coarse to adequately capture important micro-topographic processes. ATE species composition, in contrast, has a non-significant relationship with ATE elevation in the western U.S. after controlling for the effects of other abiotic variables and geographic space. This result suggests that the underlying relationships between ATE elevation and species-specific responses to climatic conditions are not dramatically different across the region. In summary, the results presented in this Chapter support the hypothesis that the ATE is fundamentally a hierarchical system in which macro-scale controls ultimately cap treeline elevation at all sites, while meso-scale and micro-scale controls influence treeline elevation by modifying coarser scale temperature and precipitation gradients.

3.9.0 References

Allen, T. F. H., and T. B. Starr. 1982. *Hierarchy: perspectives for ecological complexity*. The University of Chicago Press, Chicago.

Bader, M. Y., M. Rietkerk, and A. K. Bregt. 2007. Vegetation structure and temperature regimes of tropical alpine treelines. *Arctic Antarctic and Alpine Research* 39: 353-364.

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

—. 1997. Using GIS to model tree population parameters in the Rocky Mountain National Park forest-tundra ecotone. *Journal of Biogeography* 24: 513 - 526.

Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Aspect transformation in site productivity research. *Journal of Forestry* 691–692.

Beven, K. J., and M. J. Kirkby. 1979. A physically based, variable contributing area model of basin hydrology. *Hydrologic Science Bulletin* 24: 43–69.

Billings, W. D. 1973. Arctic and alpine vegetations: Similarities, differences, and susceptibility to disturbance. *BioScience* 23: 697-704.

—, ed. 1979. *High Mountain Ecosystems*. American Association for the Advancement of Science. AAAS Selected Symposia Series. Westview Press, Inc., Boulder, CO.

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

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

Cairns, D. M., and J. Moen. 2004. Herbivory influences tree lines. *Journal of Ecology* 92: 1019 - 1024.

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

Hair, J. F. J., W. C. Black, B. J. Babin, R. E. Anderson, and R. L. Tatham. 2006. *Multivariate Data Analysis*. Prentice Hall, Upper Saddle River, NJ.

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

Holtmeier, F. K. 2003. *Mountain Timberlines: Ecology, Patchiness, and Dynamics*. Springer, Berlin.

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

Hungerford, R. D., R. R. Nemani, S. W. Running, and J. C. Coughlan. 1989. MTCLIM: a mountain microclimate simulation model. US Forest Service Resesearch Paper INT-414.

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

—. 1998b. Worldwide positions of alpine treelines and their causes. Pages 221-229 in M. Beniston, and Innes, J.L., ed. *The Impacts of Climate Variability on Forests*. Springer, Berlin.

—. 2003. *Alpine Plant Life: Functional Ecology of High Mountain Ecosystems*. Springer-Verlag, Berlin.

Legendre, P., and M. Fortin. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80: 107-138.

Legendre, P., and L. Legandre. 1998. *Numerical Ecology*. Elsevier, Amsterdam.

Little, J. E. L. 1971. *Conifers and Important Hardwoods*. US Department of Agriculture, Washington, DC.

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

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

Malanson, G. P., D. R. Butler, D. B. Fagre, S. J. Walsh, D. F. Tomback, L. D. Daniels, L. M. Resler, W. K. Smith, D. J. Weiss, D. L. Peterson, A. G. Bunn,

C. A. Hiemstra, D. Liptzin, P. S. Bourgeron, Z. Shen, and C. I. Millar. 2007. Alpine treeline of Western North America: Linking organism-to-landscape dynamics. *Physical Geography* 28: 378-396.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27: 209-220.

Moore, I. D., R. B. Grayson, and A. R. Ladson. 1991. Digital terrain modeling - a review of hydrological, geomorphological, and biological applications. *Hydrological Processes* 5: 3-30.

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

Riaño, D., E. Chuvieco, J. Salas, and I. Aguado. 2003. Assessment of different topographic corrections in Landsat-TM data for mapping vegetation types. *IEEE Transactions on Geoscience and Remote Sensing* 41: 1056 - 1061.

Richardson, A. D., and A. J. Friedland. 2007. A review of the theories to explain Arctic and alpine treelines around the world. *Journal of Sustainable Forestry*.

Riley, S. J., S. D. Degloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences* 5: 23–27.

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

Seastedt, T. R., W. D. Bowman, T. N. Caine, D. McKnight, A. Townsend, and M. W. Williams. 2004. The landscape continum: a model for high-elevation ecosystems. *BioScience* 54: 111-121.

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

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

Tranquillini, W. 1979. *Physiological Ecology of the Alpine Timberline: Tree Existance at High Altitudes with Special Reference to the European Alps*. Springer-Verlag, Berlin.

USGS. 1999. Digital representation of "Atlas of United States Trees" by Elbert L. Little, Jr. U.S. Geological Survey.

Walsh, S. J., D. R. Butler, T. R. Allen, and G. P. Malanson. 1994. Influence of snow patterns and snow avalanches on the alpine treeline ecotone. *Journal of Vegetation Science* 5: 657-672.

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

Young, K. R., and B. León. 2007. Tree-line changes along the Andes: implications of spatial patterns and dynamics. *Philosophical Transactions of the Royal Society B* 362: 263-272.

Chapter 4

A REGIONAL SCALE, SPATIAL ANALYSIS OF ENVIRONMENTAL CONTROLS ON TREE PRESENCE AND ABSENCE WITHIN THE ALPINE TREELINE ECOTONE

4.1.0 Introduction

The Alpine Treeline Ecotone (ATE) is one of the most recognizable and frequently studied ecological boundaries. The ATE is defined as the boundary zone between subalpine forests and landcover types found upslope including tundra, bare rock, and snow and ice. ATEs range from abrupt boundaries, characterized by a line of upright trees adjacent to treeless areas, to wide boundaries hundreds of meters in width that contain intermixed patches of distinct ATE components. The spatial arrangement of trees within the ATE varies greatly in response to characteristics of the tree species comprising the ecotone and the topographic characteristics of the underlying landscape. As a result, trees within the ATE range from isolated, upright individuals, to dense patches of trees with a prostrate, shrub-like growth form.

Climatic conditions are the fundamental cause of the ATE, as tree species common in subalpine forests cannot establish and/or survive in the harsh conditions found above the ecotone (e.g., Körner 1998b). Climatic conditions, however, vary geographically as they are subject to coarse scale processes acting at regional-to-global scales (e.g., climatological influences from oceanic currents). The geographic variability in climatic conditions is reflected in spatially-contingent ATE controls, as ATEs form in mountain regions that are subject to a diverse set of climatic regimes. For example, ATEs respond differently to precipitation in moist maritime mountains than in comparatively dry continental mountains.

At finer spatial scales, coarse-scale climatic conditions alone cannot explain the spatial heterogeneity of landcover present within many ATEs. This fine-scale heterogeneity is attributable to one or more environmental conditions and/or ecological processes that create micro-sites of suitable and/or unsuitable habitat for trees. Conditions and processes hypothesized to influence the ATE at fine spatial scales include topographic effects, geomorphic processes, lithologic and pedologic conditions, and biotic interactions such as ecological feedbacks (Seastedt et al. 2004). Many of these conditions and processes effectively modify local climatic characteristics, thereby introducing fine scale details to spatial patterns that otherwise reflect broader scale conditions.

The coarse scale climatic conditions and fine scale environmental conditions and ecological processes affecting the ATE ultimately produce a complex spatial arrangement of interacting factors that is not well understood (Holtmeier 2003). Previous research focused on the specific conditions and mechanisms responsible for controlling the ATE at fine spatial scales supports the idea that ATE controls are geographically variable (e.g., Daniels and Veblen

2003). Coarser scale ATE research findings (i.e., global scale), in contrast, typically attribute ATE elevational variability to climatic effects that are fairly consistent in all places (Körner 1998a). The apparent disconnect between coarse and fine scale ATE controls illustrates that processes affecting the ATE are scale-dependent. This discrepancy also underscores the need to better understand (1) how ATE controls “scale up” from the local to the global and (2) how ATE controls vary geographically. These research topics have been addressed theoretically, most notably by Billings (1979), Seastedt et al. (2004), and Holtmeier and Broll (2005). Limited empirical research, however, has been dedicated to these topics due, in part, to the logistical and technical challenges of conducting detailed, quantitative analyses over coarse geographic areas. Furthermore, comparisons of fine scale ATE research conducted at different locations are typically limited to qualitative analyses, as the methodological approaches applied to these studies, and the datasets assembled for these studies, are typically very different.

The research presented in this Chapter will explicitly address the geographic nature of ATE controls in the western United States by applying a consistent methodological approach to data collected at a regionally distributed set of study areas. The analytical approaches used in this research consist of statistical analyses of ATE samples applied at multiple spatial scales. This approach is designed to address the following research questions: (1) Which environmental variables hypothesized to control the ATE have significant relationships with ATE tree presence?, (2) How do the relative strengths of relationships between ATE presence and environmental covariates vary when comparing individual study sites distributed over a large geographic area?, and (3) How do the statistical relationships between ATE presence and environmental covariates vary across space within individual study areas?

Assessing the geographic nature of ATE controls is scientifically interesting because the ATE is a climatically sensitive ecotone that is likely to shift and/or change as a result of climate change. Effectively predicting how and where ATE characteristics will change requires a thorough understanding of the spatial patterns of ATE controls. Results from this research will provide a rare example of an empirically based analysis of ATE controls in which geographically distant and ecologically diverse study areas can be directly compared.

4.2.0 Study Areas

The study areas for this research consist of five National Parks, distributed throughout the western United States, which all have a rich history of ATE research that serves as background for this study. The study areas are Glacier National Park, MT (GNP); Rocky Mountain National Park, CO (RMNP); Sequoia National Park, CA (SNP); and Olympic and North Cascades National Parks, WA (ONP and NCNP, respectively (Figure 4.1)). These study sites provide a wide range of ATE conditions through their relative positions on the dominant temperature and precipitation gradients in the region (i.e., south-to-north and west-to-east, respectively). These sites also differ considerably in their ATE species composition, underlying geology, and geomorphic history.

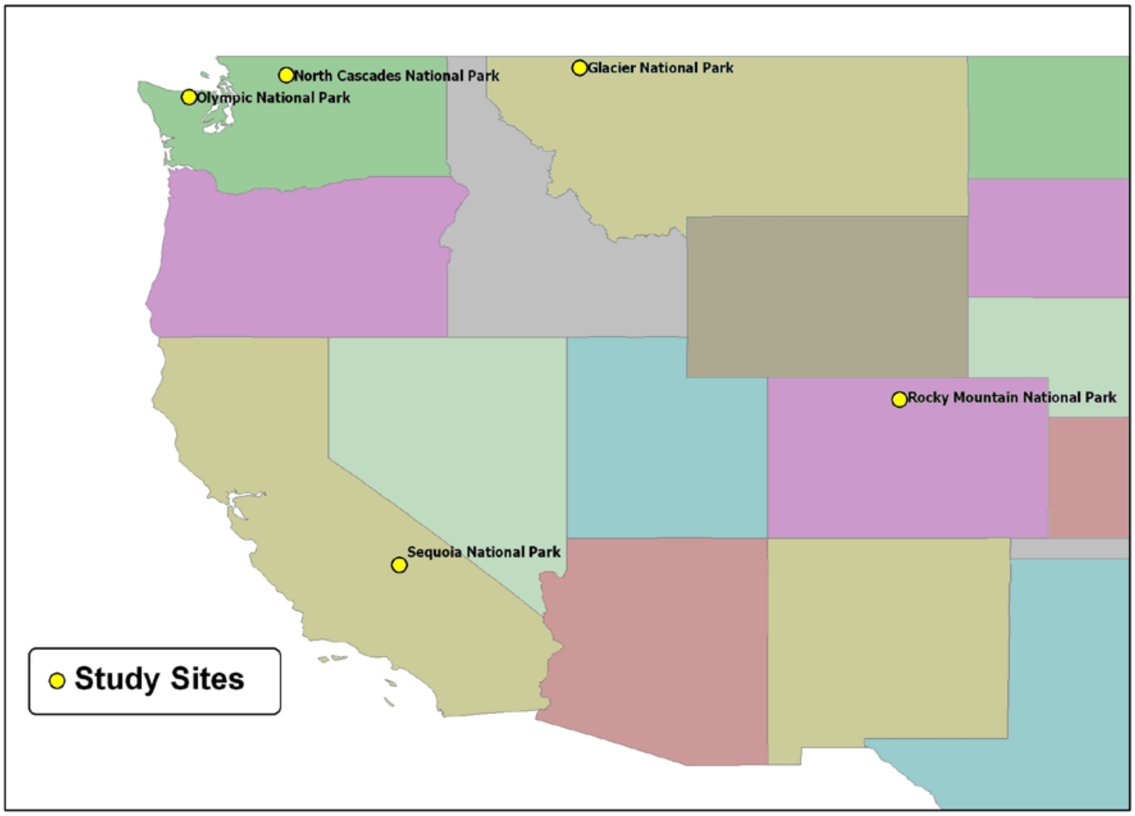


Figure 4.1: The study site distribution in the western United States.

The tree species composition of the ATE varies across the region. Some species, however, are prevalent in several of the study areas used in this analysis. For example, treelines in GNP, RMNP, ONP, and NCNP all possess subalpine fir (*Abies lasiocarpa*) as a prominent species, with Englemann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), and Douglass fir (*Pseudotsuga menziesii*) all being present at least occasionally in the ATE. Additional ATE tree species commonly found in the central and northern Rocky Mountains and/or the

Pacific Northwest include mountain hemlock (*Tsuga mertensiana*), whitebark pine (*Pinus albicaulis*), and limber pine (*Pinus flexilis*). In contrast, the ATE in SNP is dominated by Foxtail pine (*Pinus balfouriana*) with occasional occurrences of lodgepole pine and whitebark pine at treeline. The importance of species composition within the ATE is highlighted by different species adaptations for surviving in the ecotone. For example, subalpine fir and Englemann spruce readily reproduce vegetatively by sprouting roots from horizontal branches that become buried, which may eventually become new individual trees. As a result of this life strategy, fir and spruce can form self-perpetuating tree islands comprised of clones of the seedlings that originally established within the ATE. Tree patches comprised of cloned individuals are ecologically significant for the feedback processes they produce (Wilson and Agnew 1992) as, for example, they effectively become micro-topographic features that affect drifting snow (Hiemstra et al. 2002)). Foxtail pine trees in the ATE of the Sierra Nevada Mountains, however, cannot reproduce asexually, do not readily survive when forced to assume prostrate growth forms (e.g., when damaged), and tend to be found as isolated, upright individuals at treeline rather than in dense tree patches (Mastrogiuseppe and Mastrogiuseppe 1980).

With respect to the underlying geology and the geomorphic history of the primary study areas, GNP is dominated by brittle shale and mudstone that experienced significant sculpting by Pleistocene glaciation (Carrara 1989). Likewise, ATE areas in ONP tend to be composed of sedimentary rocks, although the geology of this park is more convoluted than GNP as sandstone and shale are intermixed with basalt (Tabor 1975). Mountains contained within RMNP and SNP are both dominated by granite, which provides a stable base for development of soils, establishment of plants, and resistance to erosion (including glacial scouring) (Hill 1975). Mountains in NCNP, unlike the volcanic peaks found in the southern Cascades, are composed of a composite of igneous, sedimentary, and metamorphic rocks. Many ATE areas in NCNP, however, are underlain by resistant gneiss that has characteristics similar to the granite found in RMNP and SNP (Tabor and Haugerud 1999).

4.3.0 Background

Terrestrial ecotones are scientifically interesting because they contain, within close proximity, environmental conditions that produce and support distinctly different cover types. In other words, ecotones contain ecological niche spaces for species from multiple biotic communities within spatially compact areas (Whittaker 1975). As such, ecotones can serve as natural laboratories for studying species and community competition and interaction, and for exploring abiotic and biotic conditions that produce ecological niches. The compact nature of ecotones is important because many medium-to-coarse scale environmental conditions vary relatively little at fine spatial scales, thereby allowing them to be effectively ignored or controlled for during analyses. Ecotones are also important with respect to climate change because shifts within an ecotone may be bellwethers of broad scale changes in environmental conditions (e.g., Kullman 1998). The ATE is among the most often researched ecotones due, in part, to its exceptionally compact nature and unambiguous differences between its associated landcover types.

Previous ATE research can be roughly split into two categories, distinguishable by their research foci. The first ATE research category is typified by investigations of physiological *responses* of individual trees to localized climatic conditions (e.g., Shi et al. 2007). The second prevalent ATE research theme, in contrast, places the ecotone into a landscape ecological framework and focuses on the *creation* of localized climate as the product of processes occurring at multiple spatial scales (e.g., Bunn et al. 2005b). This categorization can also be made using spatial scale, as physiological research is generally focused on processes occurring within trees in response to external conditions (e.g., Smith et al. 2003), while landscape ecological approaches are principally concerned with the position of trees (and/or treeless areas) on the landscape (e.g., Bader and Ruijten 2008).

Research focused on physiological responses of ATE trees commonly links temperature effects directly to internal tree processes. Previous research on ATE tree physiology was effectively summarized by Körner (2003), who identified five major themes for ATE formation, and concluded that research findings point towards a resource utilization hypothesis as the fundamental link between temperature and tree survival within the ATE. Smith et al. (2003), however, suggests that established trees living within the ATE are very robust and, therefore, environmental conditions conducive to tree establishment are paramount for explaining treeline characteristics. A concurrent avenue of ATE research explores ATE controls using landscape ecological principles that examine relationships between ATE character and a host of environmental conditions within the ecotone. Examples of ATE research that examine relationships between ATE character and specific environmental settings and processes include assessments of (1) relationships between ATE vegetation and snow redistribution (Hiemstra et al. 2002), (2) the importance of topographic variables on ATE vegetation patterns (e.g., Allen and Walsh 1996, Baker and Weisberg 1995), (3) the role of micro-topographic shelters on seedling establishment (Resler et al. 2005), (4) the effects of disturbances on the ATE (e.g., Walsh et al. 1994), (5) relationships between geomorphic activity and ATE character (e.g., Butler et al. 2003, Butler et al. 2004, Walsh et al. 2003), (6) the relationship between ATE landcover and soil characteristics (e.g., Malanson et al. 2002), and (7) feedback effects within the ATE (e.g., Alftine and Malanson 2004, Alftine et al. 2003, Bekker 2005, Malanson 1997, e.g., Wilson and Agnew 1992). Studies that have applied landscape ecological frameworks to the ATE do not, however, run contrary to tree physiological approaches as the environmental controls explored in them are typically considered factors that modify local climatic effects by mitigating what would otherwise be prohibitive conditions for tree growth. As in most arbitrary classification systems, the line between physiological and landscape ecological ATE analytical frameworks frequently blurs. For example, Germino et al. (2002) effectively combined these frameworks by investigating the importance of micro-site influences (i.e., topographic setting and associated landcover) on physiological processes affecting seedling survival.

There are several important gaps within the existing body of ATE research that are addressed by the research presented in this Chapter. One such gap results from the different methodological and analytical approaches applied in different ATE study areas and by different research teams. This situation is not surprising, as unrelated research questions necessitate different analytical approaches, nor is this situation unique to ATE research, but the end result is that existing research results tend to only support qualitative comparisons between sites. The research presented in this Chapter provides a mechanism for quantitatively assessing controls on the ATE by assessing treelines from across the western U.S. using comparable datasets and consistent analytical procedures.

A second notable gap in existing ATE research occurs because previous studies have traditionally taken place at either global or local scales, with much less empirically based research devoted to (1) exploring hypothesized environmental controls acting upon the ATE at intermediate scales, or (2) analyzing how these controls vary geographically. Intermediate scales of analysis, however, have been explored theoretically by Billings (1979), Seastedt et al. (2004), and Holtmeier and Broll (2005). The conceptual models put forth by these authors explain the ATE hierarchically by (1) attributing treeline elevation at coarse spatial scales (i.e. regionally to globally) to climatic conditions, temperature in particular, (2) attributing intermediate scale treeline variability (i.e., within mountain ranges) primarily to topographic interactions with climate (e.g., rain shadow effects), and (3) attributing fine scale treeline characteristics to (a) micro-site conditions such as pedogenic, lithologic, and micro-topographic conditions, and (b) micro-site processes such as feedback effects and geomorphic activity. The research presented in this Chapter tests these conceptual models empirically by analyzing data collected from ATE sites distributed across a region at different spatial scales, to identify how relationships between ATE tree presence and environmental variables vary with location, scale, and site conditions.

4.4.0 Methods

The methodological approach used in this research consists of statistical analyses of relationships between tree presence and environmental variables hypothesized to influence the ATE. This approach is similar to those used by other authors for ATE research, including Bader and Ruijten (2008) and Brown (1994b). The environmental variables used in these analyses were selected to approximate hypothesized variables put forth by Holtmeier and Broll (2005). Because the intent of this research was to compare many regionally distributed study sites using a consistent analytical approach, all datasets used in this research were (1) available for all study sites and (2) consisted of quantitative measures appropriate for the statistical analyses. As such, several of the variables identified as important by Holtmeier and Broll (2005) were not included from the analysis. Notably absent variables include details about past human activity, disturbance history, and underlying geologic conditions, all of which affect the ATE. Another concession made for this research relates to the derivation of topographic environmental variables from Digital Elevation Models (DEM). The DEMs have spatial resolutions that are less-than-ideal for capturing micro-topographic details responsible for creating suitable micro-sites for tree establishment and growth.

4.4.1 Variables & Sampling Design

The dependent variable used in analyses conducted for this Chapter is tree presence or absence, which are coded as a 1 and 0, respectively, within the dataset. Tree presence and absence were determined for randomly distributed points within the approximate ATE elevation range at each study area. The approximate ATE elevation ranges were determined empirically using field- and imagery-based ATE samples collected for the analyses presented in Chapters 2 and 3 of this dissertation (i.e., the lowest and highest elevations within these ATE datasets for each Park). Each data point was manually attributed as either a tree or not a tree using panchromatic air photographs and, where available, Ikonos multi-spectral satellite imagery. All remotely sensed datasets that were not orthorectified prior to acquisition were corrected to a RMSE of < 0.5 pixels. This step was critical for maintaining spatial continuity with other digital datasets required for this analysis. The final ATE sample sets consisted of at least 200 sample points (i.e., 100 samples of tree presence and 100 samples of tree absence) collected within the estimated ATE elevation range of each study area.

The independent variables used in this analysis consisted of topographic datasets that were generated or extracted from DEMs with a spatial resolution of 10 meters. Once created, the values for each independent variable were attributed to each sample point based on their coincident geographic locations. Variables included in this analysis were elevation; slope angle; cosine slope aspect; sine slope aspect; transformed slope aspect (derived following Beers et al. (1966) to capture SW-to-NE slope aspect moisture and temperature gradients); total, planform, and profile slope curvature; slope roughness; and topographic wetness (Beven and Kirkby 1979). These topographic variables, while far from exhaustive, capture important environmental conditions hypothesized to influence the pattern-process relationships that facilitate or preclude tree establishment and growth in the ATE.

4.4.2 Statistical Approach

A focus of this research, and the rationale behind using a coarse set of regionally distributed sample sites, is to explore the geographical nature of the relationships between tree presence within ATE and hypothesized environmental controls. To address this research intent, regression analyses were conducted at two distinct scales (i.e. for each study area and within each study area), an approach that facilitates exploration of regional and site-specific trends. This scaled analytical approach is useful for analyzing the ATE because it both fits and directly tests the hierarchical nature of the hypothesized variables defined by Holtmeier and Broll (2005) and others. Furthermore, because this research utilizes identical dependent variables, independent variables, all source datasets (i.e., data from which the variables were generated), and methodological techniques, for all study areas, results from site-specific analyses are directly comparable and enable a regional assessment of geographically distinct ecotones. As with all analyses based on regression, the findings from this research will not indicate causality. However, the results from this research can add support for important relationships between ATE elevation and environmental controls identified in previous research.

For each ATE study area the relationship between tree presence and all environmental variables is assessed using logistic regression. Logistic regression analyses, as used for this research, generate models that predict the probability that each ATE sample is coincident with trees, based on the environmental characteristics of the sample site (i.e., the independent variable values derived for each point). Within this framework, the statistical significance of each environmental variable can be tested both individually (i.e., in models that test the relationship between tree presence and single environmental variables) and in multivariate models that combine the predictive power of two or more environmental variables. Determining the most appropriate multivariate model for each study area is done using a forward stepwise procedure, whereby environmental variables are added one at a time and only retained if they lead to a significant improvement in the predictive power of the final model. This approach is similar to the one used by Bader and Ruijten (2008) for assessing hypothesized controls in tropical and subtropical treelines. Assessing the influence of environmental variables both individually and in conjunction with other variables is useful given collinearity present within the environmental variable dataset.

To explore the relationships between ATE trees and environmental variables on finer spatial scales, intra-study-area analyses use Geographically Weighted Regression (GWR) to assess how the relationships between tree presence and environmental conditions vary across space. GWR is a procedure in which unique regression models (e.g., logistic or linear) are derived for each data point (A) with the relative influence of all other points in a local kernel (B_1..B_n) being inversely related to the distance between A and B_i (Fotheringham et al. 2002). The appropriate size of the local kernel is determined empirically by iteratively testing sample sizes defined by either spatial dimensions (i.e., a fixed kernel) or the number of sample points (i.e., an adaptive kernel). Since the ATE sample points in this research were fairly evenly distributed within each study area, the appropriate kernel size was similar when set using either spatial dimensions or sample sizes as the kernel criterion. The approach ultimately selected for this research was the adaptive kernel, the size of which was determined by identifying the kernel that produced the lowest Akaike Information Criterion (AIC). GWR is preferred over other methods that quantify spatial structure in relationships between variables (e.g., analyses of spatial autocorrelation such as Moran's I) because it can accommodate multivariate data. Results from GWR include regression parameters (i.e., coefficients), and significance tests, derived for each sample point, that can be mapped to show spatial patterns in the relationships between dependent and independent variables.

4.5.0 Results – Simple Logistic Regression

Results from simple logistic regression (i.e., the relationship between tree presence and single environmental covariates) are shown in Tables 4.1 and 4.2. As expected, elevation is the variable most strongly associated with tree presence/absence within the ATE. Among the sites, elevation has the greatest relative explanatory power on tree presence and absence in ONP and GNP, and the least in NCNP. A graphical example of the relationship between elevation and the probability of tree presence in GNP is shown in Figure 4.2. This figure demonstrates that trees are common at low sites, and vice-versa, but the capacity of elevation to predict tree presence/absence decreases in intermediate elevations where trees and bare areas are more intermixed.

	GNP	RMNP	SNP	ONP	NCNP
Cosine Slope Aspect	0.014	0.000	0.030 *	0.000	0.014
Transformed Cosine Slope Aspect	0.010	0.003	0.017	0.001	0.047 **
Total Slope Curvature	0.000	0.000	0.003	0.030 *	0.001
Planform Slope Curvature	0.005	0.001	0.000	0.003	0.000
Profile Slope Curvature	0.000	0.000	0.007	0.043 *	0.001
Elevation	0.540 ***	0.472 ***	0.421 ***	0.543 ***	0.282 ***
Sine Slope Aspect	0.062 ***	0.009	0.000	0.008	0.001
Slope Angle	0.215 ***	0.007	0.164 ***	0.001	0.001
Topographic Wetness index	0.093 ***	0.004	0.025 *	0.000	0.002

Table 4.1: Nagelkerke R^2 estimates from the simple logistic regression models. Significance levels are indicated by the asterisks (* < 0.05, ** < 0.01, *** < 0.001).

	GNP	RMNP	SNP	ONP	NCNP
Cosine Slope Aspect	0.305	0.035	-0.434	-0.029	-0.295
Transformed Cosine Slope Aspect	-0.275	-0.120	-0.318	-0.063	-0.527
Total Slope Curvature	-0.002	0.012	-0.040	0.126	-0.012
Planform Slope Curvature	-0.134	0.057	0.006	0.076	-0.015
Profile Slope Curvature	-0.024	0.000	0.097	-0.215	0.021
Elevation	-0.006	-0.010	-0.007	-0.007	-0.003
Sine Slope Aspect	-0.629	-0.237	-0.027	0.015	-0.073
Slope Angle	-0.066	-0.013	-0.065	0.008	-0.006
Topographic Wetness index	0.336	0.000	0.173	0.003	0.049

Table 4.2: Coefficient values from the simple logistic regression models.

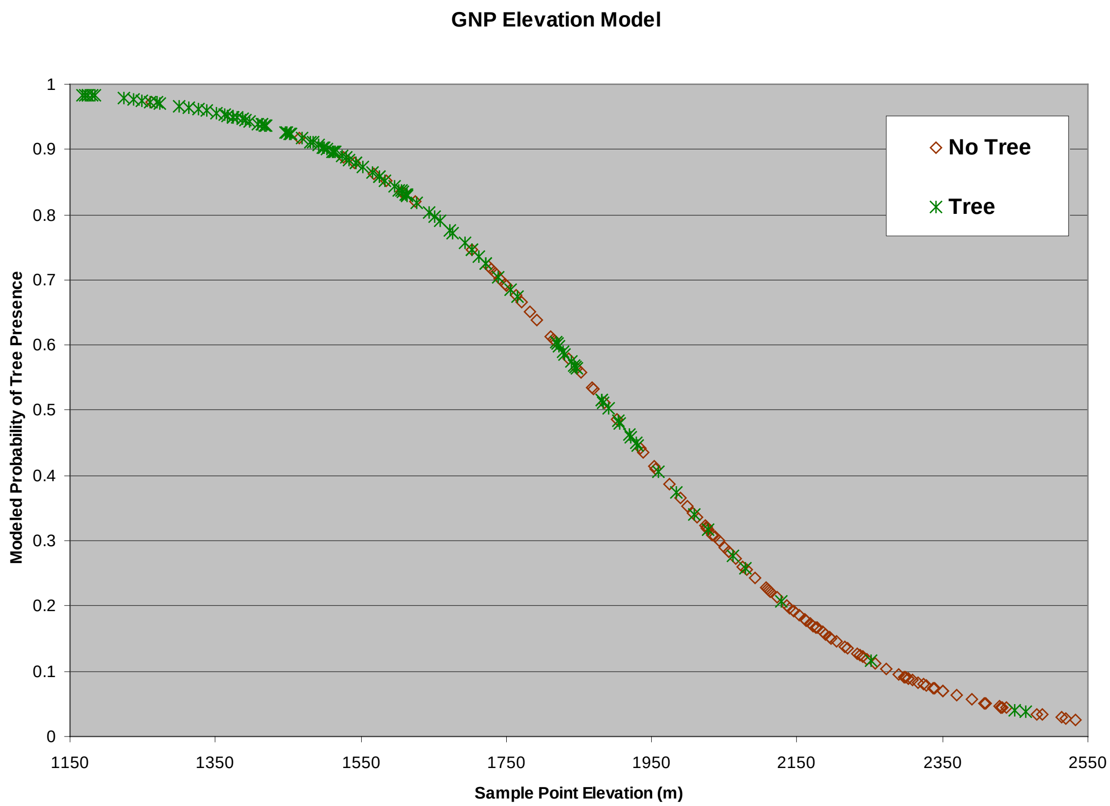


Figure 4.2: Plot of fitted probabilities of tree presence vs. sample point elevation. The colors represent actual values for samples.

Other than elevation, none of the environmental covariates tested within this research is significantly correlated with ATE tree presence at more than two study areas. At least one measure of slope aspect, however, is significant for SNP, GNP, and NCNP. The specific relationships between aspect and tree presence in these parks are interpretable using the regression model coefficients (Table 4.2), which indicate higher probabilities of tree presence on south facing slopes in SNP, southwest facing slopes in NCNP, and west facing slopes in GNP. Slope angle (i.e., steepness) is significantly related to tree presence in GNP and SNP, and these relationships have the highest Nagelkerke R^2 values among covariates other than elevation. Measures of slope curvature are the least useful for predicting ATE tree presence, and only produce a significant relationship in ONP. Interestingly, the correlation coefficient for this relationship (i.e., profile curvature vs. tree presence in ONP) was negative, suggesting that trees in this area are more prevalent in concave areas. Finally, tree presence/absence in GNP and SNP has a significant relationship with topographic wetness, and a positive coefficient for this model suggests that trees are more common in moist areas.

4.5.1 Results – Stepwise Multiple Logistic Regression

Results from the stepwise logistic regression models are shown in Table 4.3. For all study sites, the iterative stepwise procedure eliminated most of the environmental covariates derived for this analysis. With the exception of elevation, there were no environmental variables that remain in models derived for more than two study areas. However, measures of slope aspect remain in models for four of the five study sites, suggesting that (1) slope aspect is associated with tree presence/absence in most treelines, but (2) the specific influence of slope aspect is spatially variable. Slope angle and profile slope curvature remain in models for SNP and ONP, respectively, and show the same trends visible in the simple logistic regression models (i.e., steep slopes lower the probability of tree presence in SNP, and slopes with convex profile curvature lower the probability of tree presence in ONP).

Study Area	Nagelkerke R Square	Variables in the Equation	Standard Error	Wald	Significance
GNP	0.555	Elevation	0.001	72.432	0.000
		Sine Slope Aspect	0.232	5.065	0.024
RMNP	0.504	Elevation	0.001	109.695	0.000
		Sine Slope Aspect	0.197	14.484	0.000
SNP	0.574	Elevation	0.001	61.141	0.000
		Cosine Slope Aspect	0.258	17.814	0.000
		Slope Angle	0.016	20.762	0.000
ONP	0.568	Elevation	0.001	58.512	0.000
		Profile Slope Curvature	0.099	6.376	0.012
NCNP	0.334	Elevation	0.001	43.429	0.000
		Transformed Cosine Slope Aspect	0.216	11.119	0.001

Table 4.3: Nagelkerke R^2 estimates from the multiple logistic regression models. Significance levels are indicated for all variables retained during the stepwise regression procedure. Wald scores indicate the relative importance of each variable for each study area, but these scores are not directly comparable for different study areas as the ATE tree presence/absence sample sizes varied.

The results in Table 4.3 show that elevation is the variable most strongly associated with tree presence for all study areas, despite the inclusion of other environmental covariates within the logistic regression models. This assessment is made possible by comparing the Wald scores calculated for elevation to those derived for the other covariate(s). With respect to the overall predictive capacity of the models, four of the five study areas had Nagelkerke R^2 values in excess of 0.5, with only NCNP failing to achieve this level. Including multiple variables in models always produced higher Nagelkerke R^2 values than the simple models, but these improvements are modest when compared to the simple models that use elevation as the sole independent variable. For example, the largest increase in Nagelkerke R^2 value for any site was 0.099, or about 10%, which is found for SNP when comparing the simple logistic regression model for elevation with the multiple logistic regression model that also contains cosine slope aspect and slope angle. A graphical example of the influence of additional covariates is shown in Figure 4.3, which demonstrates the ability of an additional variable, in this case sine slope aspect, to modify the simple relationship between tree presence and elevation.

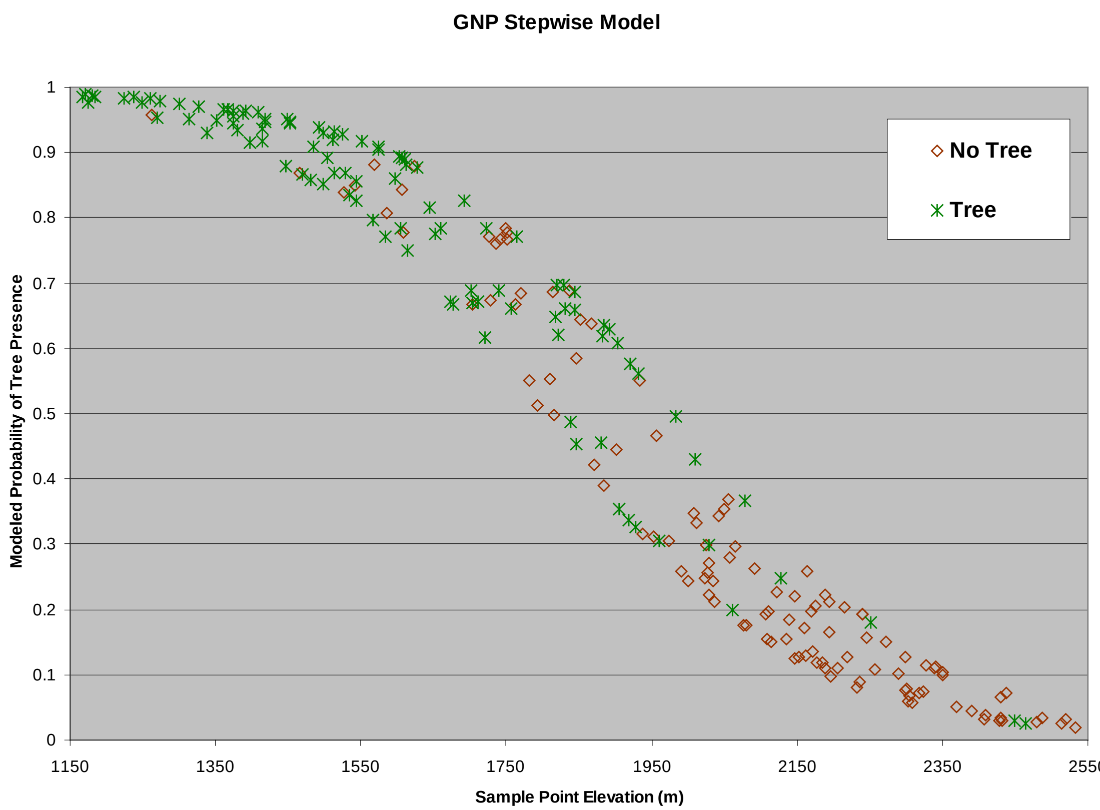


Figure 4.3: Plot of fitted probabilities of tree presence vs. sample point elevation. The final logistic regression model includes only elevation and sine slope aspect, with the influence of sine slope aspect being responsible for the scatter around the curve. The colors represent actual values for samples.

4.5.2 Results – Logistic GWR

GWR models are produced using the set of variables that remain after the stepwise procedure (i.e., those included for each site in Table 4.3). As expected, the GWR results were superior to results produced using global regression models (i.e., the GRW models produced lower Akaike Information Criterion (AIC) score) (Table 4.4). Regression parameters (e.g., coefficients and t-values) were derived for each independent variable at each samples point. Examples of geographic variability in the t-values for the relationships between tree presence and elevation are shown for GNP, RMNP, and SNP in Figures 4.4, 4.5, and 4.6 respectively. Similar maps were generated for ONP and NCNP (not shown), but did they not contain readily apparent or interpretable spatial patterns. In GNP the spatial pattern of t-values suggests that elevation is more strongly related to tree presence on the west side of the Park, although it is significantly related to tree presence Park-wide, In contrast, SNP showed the opposite trend, with t-values for elevation showing a west-to-east trend of increasing statistical significance. A second visible trend in SNP is an apparent increase in the significance of elevation as elevation increases (i.e., at higher altitudes, elevation becomes a better predictor of tree presence). This pattern was also apparent in RMNP, where elevation is not a significant predictor of tree presence in the lower reaches of the ATE, as indicated by an absolute t-value of less than 2.

	GNP	RMNP	SNP	ONP	NCNP
Non-GWR AIC	231.438053	377.119771	233.411697	199.892709	264.848175
GWR AIC	215.642653	354.593782	219.351017	188.467630	241.927048

Table 4.4: Comparison of the multiple logistic regression models and the multiple logistic GWR models derived using site-specific independent variables. In all cases the GWR models produced lower AIC scores.

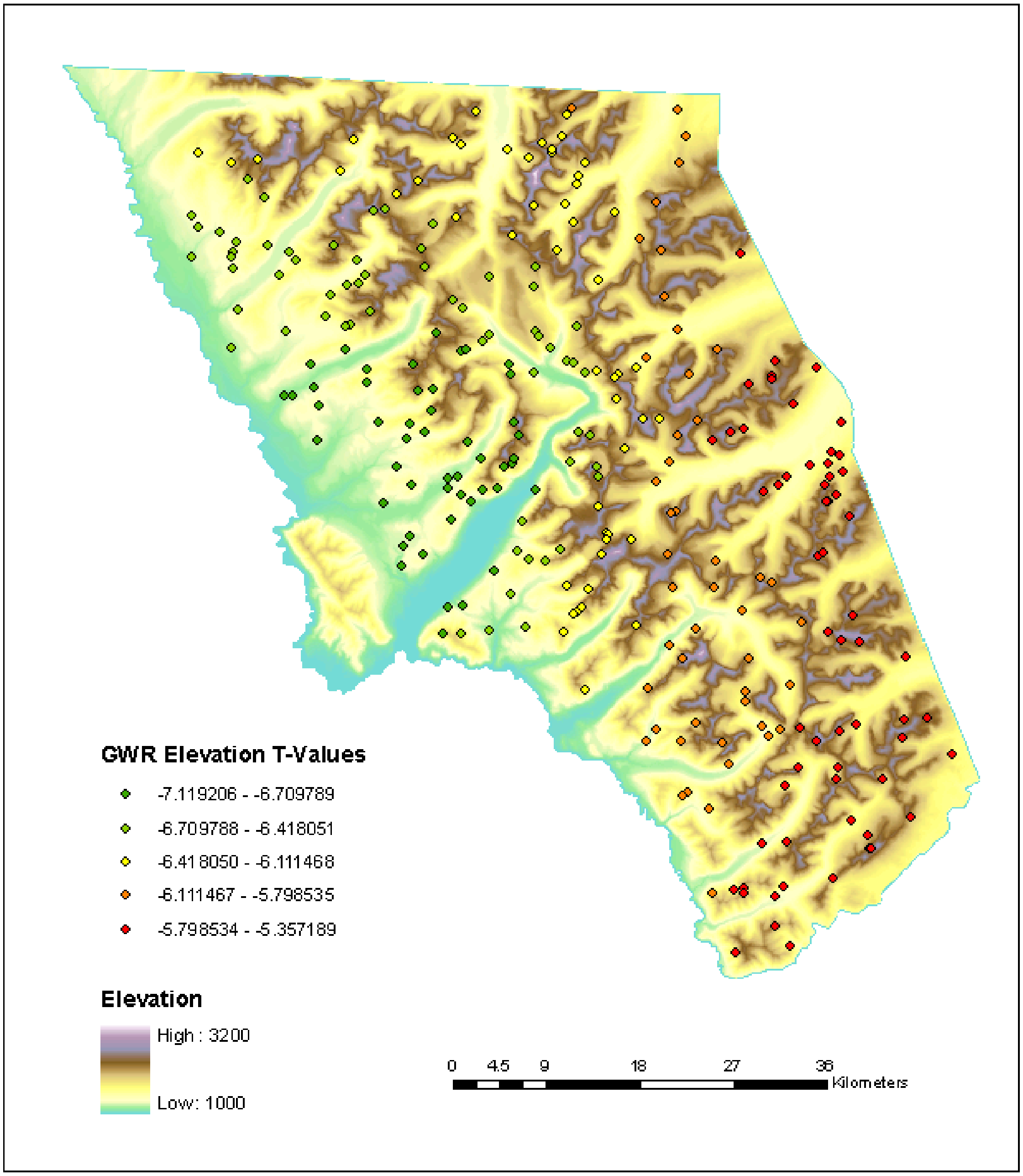


Figure 4.4: Geographic variability in the t-values for the relationship between tree presence/absence and elevation within GNP. Values for each sample point were derived using GWR models that included only the variables that remained following the stepwise regression analysis.

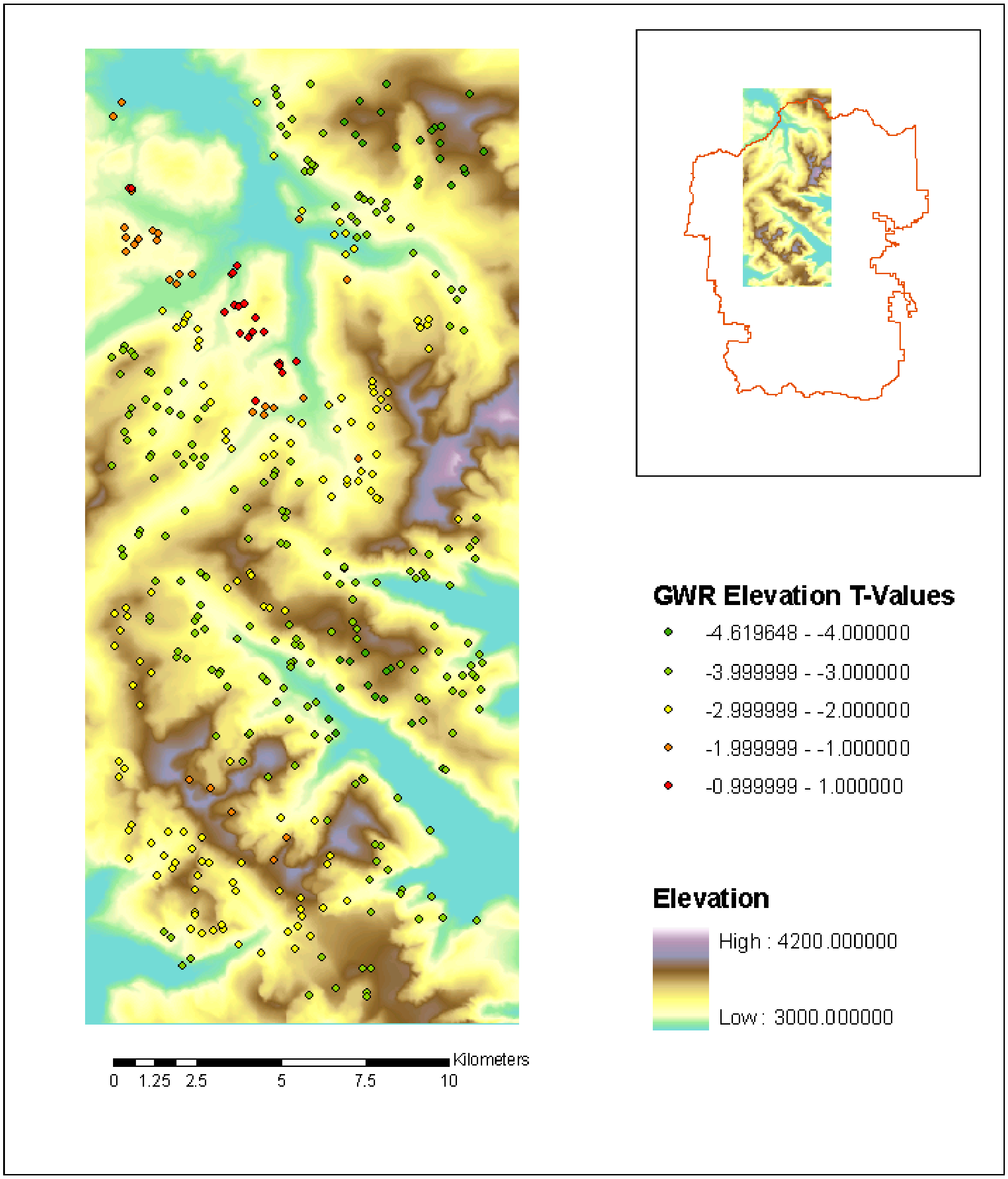


Figure 4.5: Geographic variability in the t-values for the relationship between tree presence/absence and elevation within RMNP. Values for each sample point were derived using GWR models that included only the variables that remained following the stepwise regression analysis.

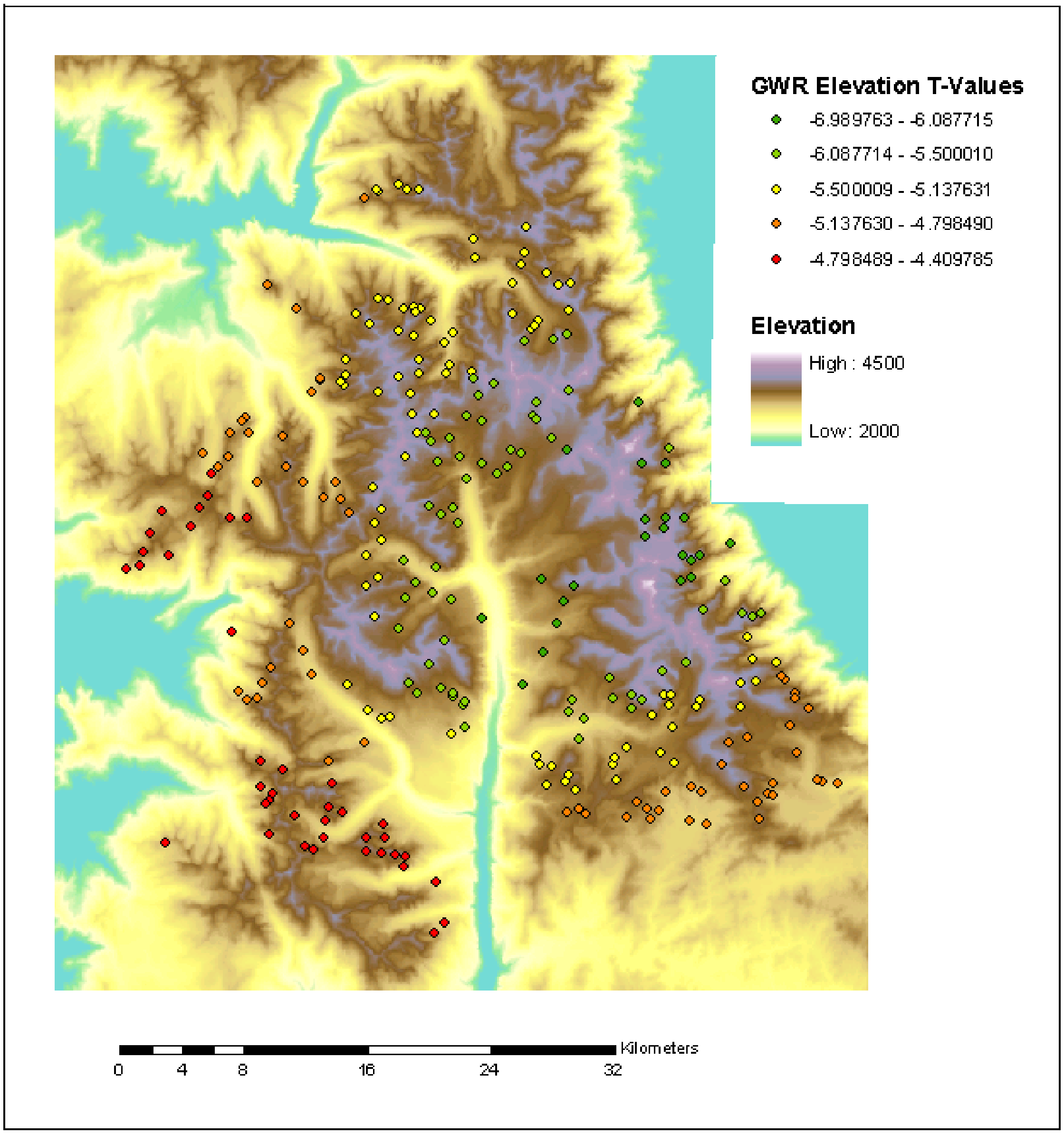


Figure 4.6: Geographic variability in the t-values for the relationship between tree presence/absence and elevation within SNP. Values for each sample point were derived using GWR models that included only the variables that remained following the stepwise regression analysis.

4.6.0 Discussion

The principal intent of the research presented in this Chapter was to explore geographic variability in the relationships between tree presence and a set of environmental variables for five regionally distributed ATE study sites. To accomplish this goal it was necessary to maintain a consistent analytical framework and identical data types for all study sites. The resulting approach provides a quantitative, empirically based means for comparing and contrasting study areas with distinct abiotic characteristics. Furthermore, this approach establishes a mechanism for better contextualizing detailed-but-site-specific ATE research within a regional-to-global understanding of ATE dynamics.

To facilitate this research, a number of compromises were made to balance (1) the desire to use the best available datasets with (2) the need to maintain data consistency across all sites. The datasets included in the analyses, therefore, are far from exhaustive and are not necessarily ideal representations of the hypothesized ATE controls they attempt to capture. These compromises lead to several notable shortcomings for the research presented in the Chapter, including (1) the lack of variables that adequately capture neighborhood effects important for tree survival, such as the position of sample points relative to adjacent topographic features (e.g., ridges) that influence the redistribution of snow; (2) an inability of the base datasets, in particular the DEMs, to adequately capture microtopographic details pertinent to ATE tree presence and absence; and (3) small sample sizes that may not have provided the requisite data volume to tease out subtle yet significant relationships. The legacy of such compromises is evident in results that do not always connect seamlessly with site specific research conducted at finer spatial scales. This research does, however, establish an analytical framework, a set of base datasets, and initial results upon which future research can be based. Examples of desirable datasets for increasing the utility of this analytical framework include topographic variables derived from higher resolution DEMs (e.g., those produced by LIght Detection And Ranging (LIDAR)) and climatic data modeled at high spatial resolutions and/or over longer time periods.

Despite limitations inherent to the base datasets, results from the analyses presented in this Chapter provide insights into regional and site-specific ATE dynamics. Most notably, results from the analyses for all study areas generally support the well established relationship between elevation and tree presence within the ATE (e.g., Körner 1998b). However, the results also suggest that the relative ability of elevation to predict tree presence within the ATE varies spatially at scales ranging from a few kilometers to the entire region. Also of interest are the relationships between tree presence and other environmental variables hypothesized to influence the ecotone, as these relationships are not consistent among the geographically distant and distinct study sites. This result supports previous research findings that identify a number of geographically variable processes, conditions, and their interacting effects that influence ATE character (c.f., Holtmeier 2003).

Other than elevation, measures of slope aspect were the variable type most frequently found to be significantly related to ATE tree presence. When a significant relationship between slope aspect and tree presence was found, as it was in GNP, SNP, and NCNP, the regression parameters indicated that warmer and/or windier sites had a higher probability of containing trees. The association between tree presence and warmer aspects fits the hypothesis that trees respond positively to warmer microsites located within an otherwise harsh environment. However, the positive relationship between west facing slopes and tree presence that was found within the GNP dataset was surprising, as current theory holds that trees in windy, continental mountain ranges such as the Rocky Mountains benefit from sheltered locations that experience greater snow accumulation (Tranquillini 1979). Furthermore, the lack of any significant relationship between slope aspect and tree presence in RMNP and ONP was surprising and may be indicative of one or more shortcomings inherent to the datasets and/or methodological approaches applied for this research.

Another finding that was somewhat surprising was the significant relationship between tree presence and profile curvature that was found in ONP. In this case, the logistic regression results suggest that trees have a higher probability of occurring in concave areas, which runs counter to field observations from this Park (see Chapter 2). The likely explanation for this discrepancy is that the curvature metric, as calculated within a 30x30 meter window moving over a 10 meter DEM, is simply measuring a slope phenomenon that fails to capture important microtopographic features influencing the ATE.

In the simple logistic regression results, slope angle (i.e., slope steepness) was significantly related to tree presence in GNP and SNP. In the stepwise regression model for SNP, slope angle remained significantly correlated with tree presence, and the regression parameters indicated that steeper slopes decreased the likelihood of tree presence. This finding makes sense as steeper areas tend to be drier and have thinner soils, which both affect tree survival by increasing the likelihood of moisture stress. In contrast, slope angle was no longer significant in the stepwise regression model produced for GNP. Exploration of the GNP dataset revealed that slope angle was dropped during the stepwise procedure because it was collinear with elevation and, therefore, little predictive power was added by the inclusion of slope angle in the presence of elevation. Collinearity among these variables is interpretable as a product of the highly glaciated environment found within GNP that is characterized by very steeply sloped peaks and valley walls. The collinearity found among environmental variables in GNP is typical of the environmental datasets derived for all study sites in this analysis, and in most datasets capturing phenomena occurring on natural environmental gradients. Furthermore, collinearity within the environmental datasets derived for each Park was ultimately responsible for all variables that were dropped within the stepwise procedure that had been significant in the simple logistic regression models.

Unlike the simple and stepwise logistic regression results that allow only rudimentary comparisons of relationships between tree presence and environmental conditions, results from the GWR analyses allow detailed spatial patterns within these relationships to be identified and interpreted. Notable results from the GWR analyses include east-to-west trends in the relative significance of elevation that were identifiable in GNP and SNP. These trends are interpretable as possible responses to the spatial distribution of snowfall, and its subsequent redistribution, occurring in these Parks. In GNP elevation was more strongly correlated with tree presence in the west than in the east, which suggests that there is less variability in ATE elevation in areas that (1) receive greater annual snowfall and (2) tend to be less windy (i.e., calmer areas west of the Continental Divide). Due to the advantages for trees produced by winter snow burial, this finding may indicate that microsites favoring snow accumulation are more important for tree establishment east of the Continental Divide in GNP. The east-to-west trend in SNP shows the opposite pattern as the probability of tree presence in the west of the Park (i.e., in areas receiving more snow due to orographic precipitation) has a weaker relationship with elevation than areas in the east. This finding may be an indication that localized areas where excessive snow accumulates and limits the number of snow free days in the growing season may be more common in the western parts of SNP. The net effect of abundant snow accumulation areas is to reduce the utility of elevation for predicting tree presence by producing tree-free areas in the lower reaches of the ecotone.

A second notable trend was visible in the GWR results produced for RMNP and SNP. In both study areas, the relative strength of the relationship between elevation and tree presence increased at higher elevations. This finding is likely indicative of higher treelines being controlled principally by climatic conditions and, therefore, being subject to greater influence by slight elevation changes and their corresponding effects on temperature. In contrast, tree presence in treelines occurring at lower elevations are more likely to be affected by processes and conditions that depress treelines (i.e., prevent them from advancing upslope to their theoretical climatic limit) and have a weaker relationship with elevation. For example, in the lower reaches of the ATE, the absence of trees is likely to be reflective of features like sheer cliffs or areas that have experienced recent disturbance and, as such, elevation alone will have little utility for predicting tree presence in these areas.

In the results from all analytical approaches, the environmental variables, with the exception of elevation, did not prove to be strongly related to tree presence within the ATE. These findings, however, do not mean that the hypothesized variables are not influential for determining the spatial distribution of tree presence. On the contrary, these results merely highlight that some variables, while appearing to be obvious ATE controls to researchers in the field, are effectively too subtle to be detected at the scales used in this analysis and/or with such a small sample size. Evidence for this assessment comes from Bader and Ruiiten (2008) who found eight variables, which were very similar to the variables used in this analysis, to be significantly related to ATE tree presence when using a large sample size derived from classified remotely sensed imagery. A large sample size would also produce more samples of isolated patches of (1) trees within otherwise treeless areas, and (2) gaps or clearings within otherwise closed-canopy forest. These relatively rare features, and the environmental conditions coincident with them, are particularly interesting to ATE researchers as examples of fine scale effects that contribute to the overall character of the ecotone.

4.7.0 Conclusion

This Chapter presents a quantitative analysis of the relationships between the tree presence within the ATE and a set of abiotic conditions hypothesized to influence tree establishment and survival. Comparable analyses were conducted at five National Parks distributed throughout the western United States to provide a diverse set of treeline conditions from which to explore key commonalities and differences. The environmental variables tested within these analyses consisted of variables identified by previous research as important influences on ATE character. Of the variables tested, elevation was the most strongly associated with tree presence, as this variable is directly related to air temperature. Other variables tested, including measures of slope aspect, slope angle, and slope curvature, had statistically significant relationships with tree presence in some but not all Parks. These findings suggest important geographic variability in the relative influence of environmental controls on ATE dynamics. Furthermore, analyses at finer scales produced results suggesting that ATE controls may be spatially variable at scales as small as a few kilometers. As such, future research on factors controlling ATE characteristics should be preceded by careful consideration of multiple environmental influences and the importance of interacting effects acting across spatial scales.

4.8.0 References

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

Alftine, K. J., G. P. Malanson, and D. B. Fagre. 2003. Feedback-driven response to multidecadal climatic variability at alpine treeline. *Physical Geography* 24: 520-535.

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

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

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

Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Aspect transformation in site productivity research. *Journal of Forestry* 691–692.

Bekker, M. F. 2005. Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, U.S.A. *Arctic, Antarctic, and Alpine Research* 37: 97-107.

Beven, K. J., and M. J. Kirkby. 1979. A physically based, variable contributing area model of basin hydrology. *Hydrologic Science Bulletin* 24: 43–69.

Billings, W. D., ed. 1979. *High Mountain Ecosystems*. American Association for the Advancement of Science. AAAS Selected Symposia Series. Westview Press, Inc., Boulder, CO.

Brown, D. G. 1994. Predicting vegetation types at treeline using topography and biophysical disturbance variables. *Journal of Vegetation Science* 5: 641-656.

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

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

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

Carrara, P. E. 1989. *Late quaternary glacial and vegetative history of the Glacier National Park region, Montana*. U.S. Dept. of the Interior, U.S. Geological Survey, Denver, CO.

Daniels, L. D., and T. T. Veblen. 2003. Regional and local effects of disturbance and climate on altitudinal treelines in northern Patagonia. *Journal of Vegetation Science* 14: 733-742.

Fotheringham, A. S., C. Brunsdon, and M. Charlton. 2002. *Geographically Weighted Regression : The Analysis of Spatially Varying Relationships*. Wiley, Chichester.

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

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

Hill, M. 1975. *Geology of the Sierra Nevada*. University of California Press, Berkeley.

Holtmeier, F. K. 2003. *Mountain Timberlines: Ecology, Patchiness, and Dynamics*. Springer, Berlin.

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

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

—. 1998b. Worldwide positions of alpine treelines and their causes. Pages 221-229 in M. Beniston, and Innes, J.L., ed. *The Impacts of Climate Variability on Forests*. Springer, Berlin.

—. 2003. *Alpine Plant Life: Functional Ecology of High Mountain Ecosystems*. Springer-Verlag, Berlin.

Kullman, L. 1998. Tree-limits and montane forests in the Swedish Scandes: Sensitive biomonitors of climate change and variability. *Ambio* 27: 312-321.

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

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

Mastrogiuseppe, R. J., and J. D. Mastrogiuseppe. 1980. A study of Pinus balfouriana Grev. & Balf. (Pinaceae). *Systematic Botany* 5: 86-104.

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

Seastedt, T. R., W. D. Bowman, T. N. Caine, D. McKnight, A. Townsend, and M. W. Williams. 2004. The landscape continum: a model for high-elevation ecosystems. *BioScience* 54: 111-121.

Shi, P., C. Körner, and G. Hoch. 2007. A test of the growth-limitation theory for alpine tree line formation in evergreen and deciduous taxa of the eastern Himalayas. *Functional Ecology* 22: 213-220.

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

Tabor, R. W. 1975. *Guide to the Geology of Olympic National Park*. University of Washington Press, Seattle.

Tabor, R. W., and R. A. Haugerud. 1999. *Geology of the North Cascades : a mountain mosaic*. Mountaineers, Seattle.

Tranquillini, W. 1979. *Physiological Ecology of the Alpine Timberline: Tree Existance at High Altitudes with Special Reference to the European Alps*. Springer-Verlag, Berlin.

Walsh, S. J., D. R. Butler, T. R. Allen, and G. P. Malanson. 1994. Influence of snow patterns and snow avalanches on the alpine treeline ecotone. *Journal of Vegetation Science* 5: 657-672.

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

Whittaker, R. H. 1975. *Communities and ecosystems*. Macmillan, New York.

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

Chapter 5

LANDCOVER PATTERNS OF THE ALPINE TREELINE ECOTONE IN THE WESTERN UNITED STATES

5.1.0 Introduction

The research presented in this Chapter explores landcover patterns in the Alpine Treeline Ecotone (ATE) of the western United States. The ATE is defined as the area between the closed canopy subalpine forest and treeless areas generally found upslope at higher elevations. The ATE in the western U.S. ranges from an abrupt edge, at which tall conifers are immediately adjacent to treeless areas, to wide ecotones characterized by patches of trees that gradually decrease in size and mean tree height with increasing elevation. Spatial patterns within this ecotone are scientifically interesting because they may be indicative of the dominant environmental controls (e.g., climatic or structurally limiting conditions) preventing trees from establishing at higher elevations (Holtmeier 2003). The underlying intent of this research is to derive a typology of fundamental ATE patterns applicable for a large and diverse geographic region, associate the resulting ATE types with those described in the literature that were defined though field-based observations, and explore the statistical relationships between each ATE type and a set of environmental variables hypothesized to influence the ecotone.

One of the central tenets of landscape ecology is the causal relationship between patterns visible on the landscape and ecological processes that are mediated by abiotic conditions at multiple spatial scales (Turner 1989). Associating pattern and process, however, is often challenging because numerous ecological processes, and complex interactions between them, may all influence landscape pattern (Levin 1992). Furthermore, the spatially variable and multi-scaled nature of landscape patterns and the process(es) responsible for producing them (Wiens 1989) lead to analytical challenges when assessing landscape patterns. Challenges of scale are exacerbated because commonly available datasets (e.g., remotely sensed imagery) often lack the requisite resolution(s) for adequately measuring landscape patterns and/or delineating the landcover types of interest. The net result is that few existing studies have associated landscape patterns with ecological processes, or the abiotic conditions coincident with them, over large study areas (i.e., at regional-to-global scales).

This research addresses the need for broad scale analysis of landscape patterns, while also contributing to the literature through an empirical analysis of regional ATE pattern-process relationships. The ATE is an ecotone amenable to the study of pattern at the scale of the region because its basic definition (i.e., the upper altitudinal edge of the forest) is geographically consistent. The ATE is also an advantageous area in which to study landscape patterns because the fundamental landcover types comprising the ecotone (i.e. trees and/or tree patches within a background of treeless landcover types) can be effectively distinguished from remotely sensed imagery (e.g., Wilson and Franklin 1992). ATE patterns, however, are variable at all spatial scales (Malanson 2001), and any analyses of pattern will be constrained by the spatial resolution of the input data. A related consideration is that all pattern typologies represent an attempt to place an infinitely variable natural phenomenon into an arbitrary typology for ease of analysis and interpretation. While important to note, these caveats do not prevent this research from contributing to the greater understanding of ATE dynamics as it represents a first attempt to quantify 2-Dimensional (2-D) ATE patterns at the scale of a region. Furthermore, this research is the first to explore geographic variability in ATE patterns across a diverse, regionally distributed set of study sites.

The questions addressed by this research are: (1) Can alpine treeline vegetation patterns be clustered into a typology that (a) is a robust classifier of treeline pattern at all study sites, and (b) matches existing ATE research findings and theoretical understandings?, (2) Are the geographic distributions of ATE types consistent with field observations of ATE characteristics from each study site?, (3) What environmental variables are associated with each treeline pattern type?, (4) Do relationships between ATE pattern and environmental conditions vary geographically across the western U.S.?, and (5) Is there evidence to support the hypothesis that treelines are polygenic in nature? Patterns likely to emerge include abrupt treelines, wide ecotones (i.e. hundreds of meters in width) with an open canopy structure, and several types of intermediately sized ecotones characterized by different patch sizes and spatial configurations (Holtmeier 2003). Examples of associations between ATE patterns and environmental controls include abrupt, orographically-controlled treelines that are expected to repeat for ATE sites across the region; and climatic treelines, for which characteristics of treeline pattern at fine scales will likely correlate most strongly with measures of micro-topography (e.g., surface roughness and slope curvature). Specific pattern-environment associations likely to occur include (1) wide treelines in gradually sloping areas, (2) abrupt treelines on steep slopes, and (3) patch sizes reflecting the size of micro-topographic features for treelines in areas with complex topography.

5.2.0 Study Area

The study areas for this research consist of 26 sites distributed throughout the western United States (Figure 5.1). These sites include five National Parks, which serve as primary study sites, and twenty-one secondary sites that provide a more complete regional context for this research by providing sampling points in areas between the primary sites. The primary and secondary sites are differentiated by the density of ATE samples collected at each, and by the amount of fieldwork conducted in each site. The sites are described more thoroughly in Chapters 1-4.

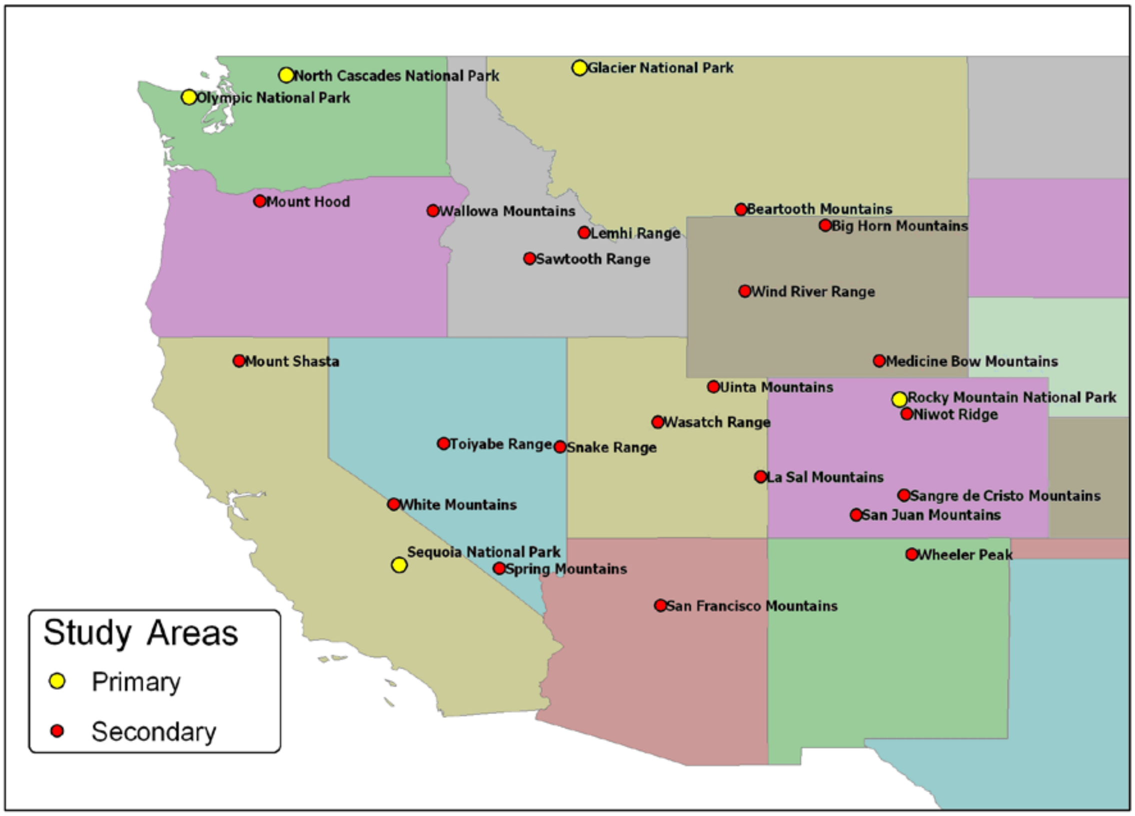


Figure 5.1: Geographic distribution of study areas for this research.

5.3.0 Background

The underlying hypothesis for this research is that ATE patterns are indicative of the environmental factors most responsible for producing the ecotone at each study site. The theoretical framework for this research was provided by (Holtmeier 2003), who described a general ATE typology, based on ATE controls, and concluded that treelines can essentially be categorized as either climatically- or orographically-controlled. Within this framework, treelines affected by disturbance are placed in the orographic category because they are often associated with (1) structurally-controlled snow avalanches, and/or (2) structural controls that influence forest fire spread. The research presented in this Chapter will build on Holtmeier's simple typology by distinguishing and differentiating ATE types found in the western U.S. and associating each type with specific environmental conditions hypothesized to influence the ecotone.

Several notable analyses of ATE pattern have previously been conducted in the western U.S. Examples include research conducted by Allen and Walsh (1996) in Glacier National Park, and by Baker and Weisberg (1995) in Rocky Mountain National Park. These studies provide important insights into the relationships between localized environmental settings (i.e., climatic and topographic conditions) and treeline pattern characteristics. However, these analyses were restricted to individual National Parks and, therefore, cannot address regional variability in ATE patterns. In contrast, analysis conducted by Daniels and Veblen (2003) in Patagonia provides a rare example of an ATE pattern assessment that spans multiple sites within a region. Another notable research project was conducted by Bader et al. (2007), which explored the relationship between tree height, vegetation character, and temperature for 1-dimensional altitudinal transects from seven ATE areas distributed in tropical and subtropical regions distributed around the Pacific Rim. To date, however, no published studies have analyzed 2-D ATE pattern over as large and diverse an area as the western U.S.

5.4.0 Methods

The methodological approach utilized in this research consists of the following steps: (1) acquisition and pre-processing of digital datasets, including Landsat imagery, panchromatic air photos, and Digital Elevation Models (DEM) for each study site; (2) classification of the Landsat imagery into basic landcover types found in the ATE throughout the region; (3) creation of randomly distributed belt-transect ATE samples that capture cross sections of the ecotone; (4) derivation of landscape pattern metrics that quantify local ATE landcover patterns for each belt-transect sample; (5) derivation of DEM-based variables that capture local topographic characteristics of each belt-transect sample; (6) creation of an ATE landcover pattern typology through the application of clustering techniques; and (7) association of ATE types with topographic variables using simple descriptive statistics and Classification And Regression Trees (CART). Critical components of this analytical framework include selecting the landcover types included in the imagery classification, applying an objective and appropriate sampling methodology for the belt transects, selecting landscape pattern metrics that effectively capture important ATE characteristics, and identifying DEM-based topographic variables that approximate topographic effects hypothesized to influence the ATE.

An important pre-processing step for this research was illumination correction, which was performed for all satellite images to compensate for unequal amounts of incident solar radiation that result from the spatially variable relationship between topographic slope aspect and solar angle. The C-correction approach (Riaño et al. 2003, Teillet et al. 1982) was the illumination correction technique utilized in this research. C-correction is an empirically based technique in which pixel brightness, in each spectral band, is regressed on the cosine aspect of the underlying slope. All pixels in the image are then corrected using the slope of the regression line as the adjustment factor. The net result of this procedure is a visual flattening of the image and a more uniform image from which to classify landcover. The C-Correction method was selected over alternatives (e.g. the cosine correction or the minaret correction) because it is an image specific, empirically based procedure that does not require any arbitrary correction coefficients.

The landcover classes selected for inclusion in the classification were chosen to capture fundamental landcover types comprising the ATE that are applicable to all study areas in the region. The classes are: conifer trees, herbaceous landcover such as tundra and alpine meadow, bare rock, and water. Other notable classes include deciduous trees and shrubs, and snow and ice. Deciduous vegetation was included within the herbaceous landcover class due to its spectral similarity and spatial association with herbaceous cover (i.e., deciduous shrubs often co-occur with herbaceous landcover in the ATE on snow avalanche paths and as willow patches within alpine tundra). Snow and ice are placed in the bare-rock category because all of the images, while collected during the growing season, do not necessarily represent completely snow-free conditions, and late-lying snow patches are assumed to be underlain principally by bare-rock. The inclusion of permanent and semi-permanent snow and ice within the bare rock class is also appropriate from a tree-limitation perspective as late-lying snow patches, and structural features such as talus slopes and sheer cliffs, are products of topographically conducive settings (Billings and Bliss 1959). An important caveat related to the classification scheme is the effect of mixed pixels (i.e., image pixels containing multiple landcover types). Given the spatial resolution of the classified imagery (i.e., 30-meter pixels) and the spatial heterogeneity of the ATE, a large proportion of pixels contained in the ATE belt-transect samples will be mixed. This is an unavoidable consequence of conducting a regional scale analysis based upon classifications of available multispectral imagery. However, this limitation is mitigated, somewhat, because the spatial configuration of image pixels (pure and mixed) may produce a reasonable ATE typology given the belt-transect sampling method (i.e., sample positions are not dependent upon the classified images and each sample captures a standardized unit of the ATE at all sites) (described in detail below).

An unsupervised classification (i.e., isodata) approach was selected for classifying landcover, and individual classifications were applied to all study areas. Post-classification attribution was performed to associate one of the predefined ATE landcover types with each spectrally separable class. Field samples (n=997) served as the reference dataset for class attribution for the five primary study areas, and one-meter spatial resolution, panchromatic Digital Orthophoto

Quadrangles (DOQ) were used for class attribution for the secondary sites. Following classification, accuracy assessments were applied for each study area (Table 5.1). Table 5.2 provides a more detailed accuracy assessment for the primary study areas. Validation data for the accuracy assessments consisted of DOQs and 4-meter spatial resolution multispectral Ikonos imagery. The accuracy of the classifications was generally high, which was expected given the simple classification scheme, but also reassuring as it suggests that the pattern analysis will not be strongly influenced by misclassified pixels.

Site	**Overall Accuracy**	**Kappa**
Glacier National Park	91%	0.86
Rocky Mountain National Park	91%	0.86
Sequoia National Park	92%	0.89
Olympic National Park	93%	0.87
North Cascades National Park	88%	0.82
San Francisco Mountains	95%	0.89
Mount Shasta	82%	0.72
White Mountains	87%	0.79
Niwot Ridge	92%	0.87
Sangre de Cristo Mountains	90%	0.86
San Juan Mountains	90%	0.85
Lemhi Mountains	92%	0.88
Sawtooth Range	88%	0.83
Beartooth Mountains	93%	0.91
Snake Range	78%	0.65
Spring Mountains	73%	0.56
Toiyabe Range	90%	0.85
Wheeler Peak	90%	0.83
Mount Hood	90%	0.84
Wallowa Mountains	80%	0.71
La Sal Mountains	83%	0.75
Uinta Mountains	87%	0.81
Wasatch Range	77%	0.65
Bighorn Mountains	83%	0.74
Medicine Bow Mountains	90%	0.85
Wind River Range	85%	0.79

Table 5.1: Accuracy assessment results for landcover classifications performed for each study area.

GNP		Water	Bare	Herb	Tree	Producers Accuracy	Overall Accuracy	Kappa
	Water	7	0	0	0	100.0%	91.4%	0.86
	Bare	0	44	5	1	88.0%		
	Herb	0	3	60	5	88.2%		
	Tree	0	2	6	123	93.9%		
	Users Accuracy	100.0%	89.8%	84.5%	95.4%			
RMNP		Water	Bare	Herb	Tree	Producers Accuracy	Overall Accuracy	Kappa
	Water	5	0	0	0	100.0%	91.3%	0.86
	Bare	0	48	6	3	84.2%		
	Herb	0	2	35	1	92.1%		
	Tree	1	0	7	122	93.9%		
	Users Accuracy	83.3%	96.0%	72.9%	96.8%			
SNP		Water	Bare	Herb	Tree	Producers Accuracy	Overall Accuracy	Kappa
	Water	20	0	0	0	100.0%	92.4%	0.89
	Bare	0	62	1	3	93.9%		
	Herb	0	0	18	1	94.7%		
	Tree	0	2	6	58	87.9%		
	Users Accuracy	100.0%	96.9%	72.0%	93.6%			
ONP		Water	Bare	Herb	Tree	Producers Accuracy	Overall Accuracy	Kappa
	Water	5	0	0	0	100.0%	93.1%	0.87
	Bare	0	22	3	2	81.5%		
	Herb	0	0	24	0	100.0%		
	Tree	0	3	3	97	94.2%		
	Users Accuracy	100.0%	88.0%	80.0%	98.0%			
NCNP		Water	Bare	Herb	Tree	Producers Accuracy	Overall Accuracy	Kappa
	Water	3	0	0	0	100.0%	88.4%	0.82
	Bare	0	55	7	3	84.6%		
	Herb	0	0	40	7	85.1%		
	Tree	0	0	10	108	91.5%		
	Users Accuracy	100.0%	100.0%	70.2%	91.5%			

Table 5.2: Full accuracy assessment error matrix for the primary study areas.

The sampling approach selected for this research was based on the belt-transect technique used to sample the ATE in Rocky Mountain National Park described by Baker and Weisberg (1995). Daniels and Veblen (2003) applied a similar sampling methodology in their study of ATE in the Patagonian Andes. This approach consisted of manually digitizing cross-ecotonal transects on high spatial resolution remotely sensed imagery. For this research, a total of 1006 belts transects were drawn perpendicular to the ATE, with each transect extending 50 meters upslope from the highest identifiable tree or tree patch and 50 meters downslope into the closed canopy subalpine forest found below the ecotone. Belt transects were extended above and below the ecotone to capture important aspects of the underlying environmental template that are hypothesized to affect ATE characteristics (e.g., cliffs immediately above the highest tree). Belt transect width for this research was determined empirically by assessing the scale-dependent relationship between vegetation patterns and transect width (Figure 5.2). Like the analysis used in this Chapter, the procedure for selecting transect width relied upon derived pattern metrics. However, high spatial resolution Ikonos imagery was used in place of Landsat imagery for this task because comparable tests performed using classified Landsat imagery did not show a distinct range at which ATE patterns stabilized. Furthermore, the transect width selected for this research (i.e., 300 meters) rarely captures major slope breaks (e.g., ridgelines) that potentially separate ATE areas controlled by different environmental processes.

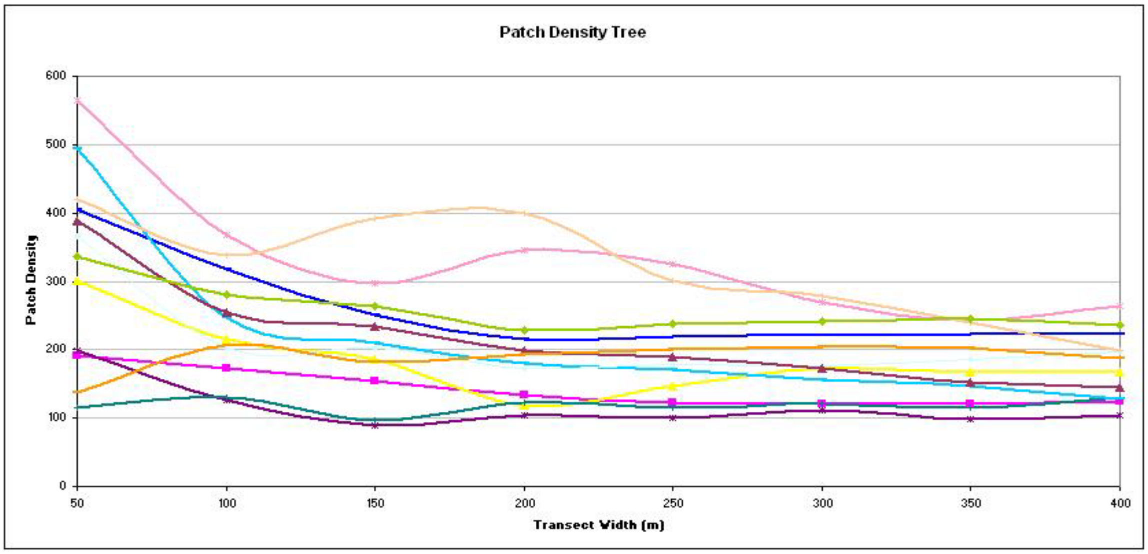


Figure 5.2: Belt-transect width determination based upon randomly selected ATE samples. Eleven samples are highlighted in this graph, each represented with a different color. The selected pattern metric, patch density, stabilizes with a transect width of approximately 300 meters.

Numerous metrics have been developed for quantifying different elements of landscape patterns (O'Neill et al. 1988). A limited set of these pattern metrics was selected for this analysis following the suggestions of Riitters et al. (1995). Selected metrics capture the fundamental characteristics of ATE pattern including the size, shape, spatial arrangement, and abundance of landcover patches. Although measures of pattern are often correlated, the pattern metrics selected for this research were carefully chosen to capture independent aspects of ATE pattern. The set of pattern metrics included patch density, radius of gyration, fractal dimension, contagion, and aggregation index. These metrics were all calculated at the landscape level (i.e., one value for each pattern metric for each ATE sample). The measures of radius of gyration and fractal dimension, however, were derived from patch based metrics, and landscape-level values for these metrics consist of class distribution statistics calculated from all patches within individual transects. Class distribution statistics collected for radius of gyration and fractal dimension include the mean, area weighted mean, and coefficient of variation. These three summary statistics are included in the analysis because each captures a different aspect of ATE character. The mean value is the simple average value for all patches. The area weighted mean weights each patch's contribution to the landscape value according to the size of the patch. This measure is distinct from the simple mean because it reduces the influence of small patches and highlights the characteristics of larger patches within the sample polygon. Within the ATE belt transect samples, large patches consist primarily of the upper edge of the subalpine forest and areas of bare rock at the upper limit of the ecotone. The coefficient of variation is a standardized measure that captures variability in the patch-based pattern metric results. Also included in the analysis are the percentages of each land type present in the belt transects. The combination of pattern and landscape composition provides the essential data that are intuitively used to attribute observed ATE patterns to ecological processes. Descriptions of the selected pattern metric and landcover composition variables are based on those provided within FRAGSTATS (McGarigal and Marks 1995) and are shown in Table 5.3.

Metric	Description
Patch density	Patch density is the number of patches divided by the total landscape area. This metric will be high in landscape with many small patches and low in landscapes with few coarse patches.
Mean Radius of gyration distribution	The mean radius of gyration is the distance between each cell in a patch and the patch centroid, averaged for the entire sample. This metric captures patch extent, but, unlike patch density, it incorporates patch size and patch compaction.
Radius of gyration distribution (AWM)	The area weighted mean of the radius of gyration also captures patch extent. The relative contribution of each patch in a landscape is weighted by the patch size, thereby highlighting characteristics of coarse patches.
Radius of gyration distribution (CV)	The coefficient of variation of the radius of gyration is calculated to assess how variable patch extent is within single ATE samples. This metric indicates whether the patches within a sample are similar or different with respect to their extent.
Fractal dimension distribution (mean)	The fractal dimension quantifies mean shape complexity for the patches in the ATE samples. This metric is conceptually similar to the perimeter-area ratio, but it has the added advantage of accounting for shape complexity across a range of scales.
Fractal dimension distribution (AWM)	The area weighted mean fractal dimension also quantifies the shape complexity within the ATE, but is weighted to place more emphasis on the coarse patches within the ecotone (i.e., the upper edge of the closed canopy subalpine forest and the primarily bare or herbaceous cover typically comprising the upper elevations of the ecotone).
Fractal dimension distribution (CV)	The coefficient of variation of the fractal dimension is calculated to quantify the patch shape variability within the individual ATE samples.
Total core area	The area of patches within the ATE samples not located on edges between landcover types. This metric combines patch size and complexity as, for example, samples with high amounts of core area will typically contain patches that are coarse and have simple shapes.
Contrast weighted edge density	Contrast weighted edge density quantifies the number of edges between landcover patches, with each edge given a weight according to user-defined values. In this analysis, the contrasts between trees and herbaceous cover, and herbaceous cover and bare rock, were both given a value of 1. The relationship between trees and bare rock, however, was given a weight of 2. These values were selected to help distinguish ATE samples that transition directly from trees to bare rock from those with ecotones containing an intermediate zone of herbaceous landcover.
Contagion	Contagion is used to characterize the spatial distribution of landscape patches within each sample. Samples that have low contagion values have more disaggregated patches and vice-versa.
Aggregation index	The aggregation index is a measure of patch contiguity summarized for all patch types. Unlike contagion, the aggregation index focuses only on like adjacencies (i.e., adjacent cells of the same landcover class).
% Bare	The percentage of the ATE sample containing bare landcover (includes snow and ice).
% Herbaceous	The percentage of the ATE sample containing herbaceous landcover (includes deciduous trees and shrubs).
% Tree	The percent of the ATE sample containing coniferous trees.

Table 5.3: Descriptions of pattern and landscape composition metrics used to differentiate ATE patterns types. Acronyms include Area Weighted Mean (AWM) and Coefficient of Variation (CV)

A treeline typology was produced from the ATE pattern and composition measures using cluster analysis. This approach is similar to the methodology used by Allen and Walsh (1996) to develop an ATE typology for Glacier National Park through clustering ATE samples based upon pattern metric analysis of classified Landsat imagery. The method selected for clustering the treeline samples is k-means clustering, a technique that partitions observations in multidimensional space to maximize between-cluster variance, while minimizing within-cluster variance. Prior to clustering, all pattern metric results were rescaled using z-scores. The appropriate number of clusters used for the analysis was determined by graphing the within-cluster sum of squares (i.e., the sum of squares of distances between all points and their assigned cluster centers) against the number of clusters. Six clusters were used for this analysis, as determined by the noticeable change in slope in the graphed line in Figure 5.3. Following clustering, the treeline typology was manually interpreted to assess which landscape features were represented by each ATE type, and to qualitatively describe the pattern types with respect to the pattern metric and landscape composition measures.

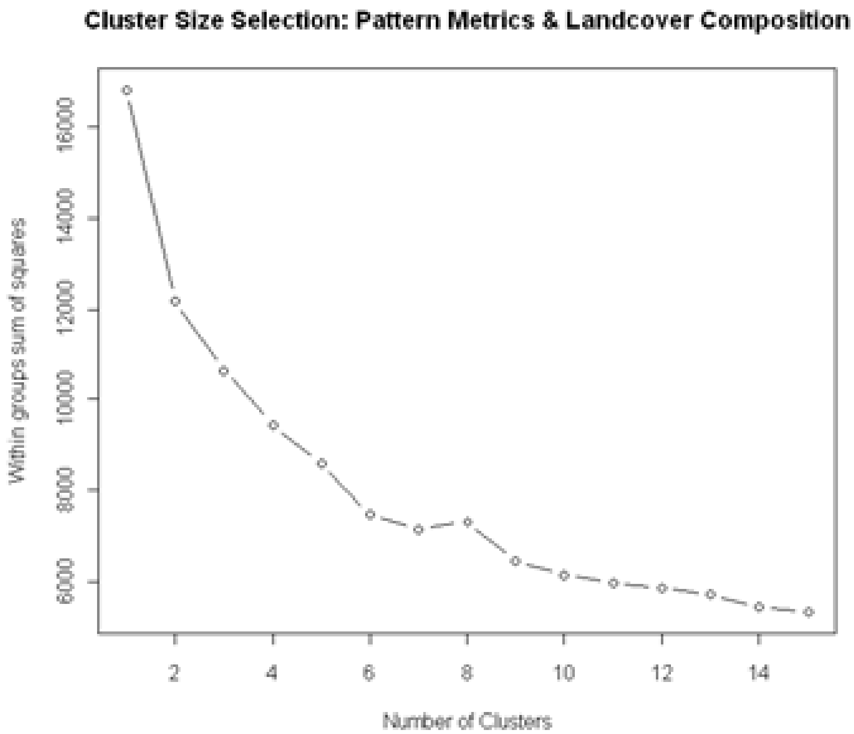


Figure 5.3: The relationship between the number of clusters and the relative compaction of sample data points around the cluster centroids. Note the difference in the slope of the line between cluster sizes 2-6, compared to the slope of the line between cluster sizes 6-15.

The environmental variables selected for inclusion in this analysis consist of topographic variables, derived from DEMs, which are designed to capture characteristics of the landscape that influence ATE patterns at all study sites. These variables are restricted to topographic conditions because, although climatic conditions are fundamental controls on ATE elevation, ATE pattern is often responsive to direct topographic limitations (e.g., structural controls like cliffs or geomorphic features) and/or fine scale interactions between topographic features and ATE vegetation (e.g., Butler et al. 2003, Butler and Walsh 1990, Holtmeier and Broll 1992). Furthermore, topographic variables have demonstrated utility for explaining the presence and/or character of ATE vegetation (Bader and Ruijten 2008, Brown 1994b). The variables used for this research were slope angle, slope aspect (cosine and transformed), belt transect elevation range, slope curvature (planform and profile), and topographic roughness. Mean belt transect slope angle is included in this analysis because steep slopes typically experience more mass movement events than gentler slopes (i.e., geomorphic controls on the ATE), and they possess few sites conducive for soil development and/or tree establishment (Butler and Walsh 1994). Mean cosine slope aspect and mean transformed slope aspect (Beers et al. 1966) were included to test the relationship between ATE pattern and aspect dependent temperature differences. Belt transect elevation range is included to capture the total relief from the top to the bottom of the ecotone and, therefore, provide a measure of ecotone abruptness. Mean slope curvature measures are included because curvature is related to winter snow depth, as greater accumulation typically occurs in concave areas. Mean slope roughness is included because it captures features that may provide micro-sites of acceptable tree habitat, above the closed-canopy subalpine forests, that facilitate the establishment of tree patches within the ATE (e.g., Butler et al. 2004, Resler et al. 2005).

Relationships between ATE types and environmental variables are explored using simple descriptive statistics and CART. Geographic variability in the association between ATE patterns and topographic conditions are explored by comparing the relationships between pattern and topographic variables for the full set of ATE samples and for subsets of the ATE samples from only primary study sites. This combined regional and site-specific analytical framework is used to test the hypothesis that treeline patterns are polygenic (e.g., that similar environmental conditions produce different patterns and/or that similar patterns arise under different environmental conditions). CART is used to test the overall ability of the topographic variables to predict ATE pattern types, and to identify the independent variables that most efficiently delineate the treeline types. CART is useful for this analysis because it is a non-parametric statistical methodology that can incorporate categorical data (e.g., the ATE types) as independent and/or dependent variables (Breiman et al. 1984).

5.5.0 Results

Based upon the relationship between the number of clusters and the cluster sum of squares (Figure 5.3), six clusters were produced using the k-means clustering algorithm. These clusters effectively provide an objective, pattern-based typology for ATE types across the western United States. The relationships between each cluster center and the pattern metrics used to produce the typology are shown in Table 5.4. Qualitative interpretations of the clusters (Table 5.5) were created to attribute meaningful descriptions of the ATE types captured within the pattern analysis by (1) describing the relationships between the clusters types and pattern metric results shown in Table 5.3, and (2) examining actual belt transect samples contained in each cluster. Examples of classified ATE samples for each type are shown in Figures 5.4 – 5.9.

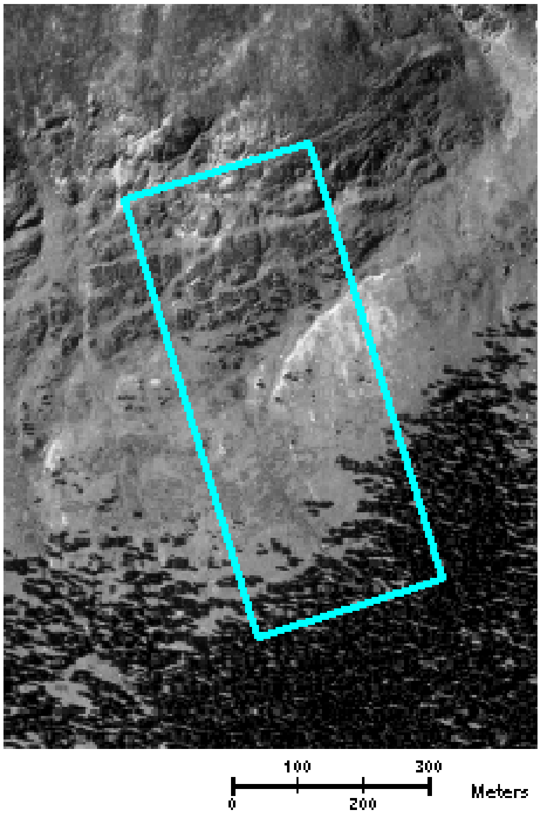
Pattern Metric	**Cluster 1**	**Cluster 2**	**Cluster 3**	**Cluster 4**	**Cluster 5**	**Cluster 6**
Patch density	-0.552	-0.972	-0.301	-0.512	-0.032	1.063
Radius of gyration distribution (mean)	0.135	1.749	-0.268	-0.083	0.045	-0.660
Radius of gyration distribution (AWM)	0.042	-0.501	0.090	2.675	0.057	-0.641
Radius of gyration distribution (CV)	0.044	-1.502	0.283	2.145	0.117	-0.272
Fractal dimension distribution (mean)	-0.308	1.157	-0.688	-0.535	0.534	-0.320
Fractal dimension distribution (AWM)	-0.385	-0.934	-0.707	1.129	0.918	-0.264
Fractal dimension distribution (CV)	-0.314	-1.502	-0.434	0.479	0.840	0.023
Total core area	-0.161	-0.664	-0.226	2.465	0.273	-0.448
Contrast weighted edge density	-0.962	-0.911	-0.565	-0.328	0.554	0.752
Contagion	0.665	0.260	1.124	0.398	-0.636	-0.576
Aggregation index	0.741	1.037	0.861	0.058	-0.796	-0.521
% Bare	-1.047	-0.106	1.471	-0.134	-0.207	0.034
% Herbaceous	1.273	-0.118	-1.047	0.513	0.219	-0.436
% Tree	-0.215	0.320	-0.684	-0.512	-0.001	0.534
Within cluster sum of squares	1001.526	1173.281	1046.660	793.356	1688.740	1627.509
Count	148	105	152	68	276	257

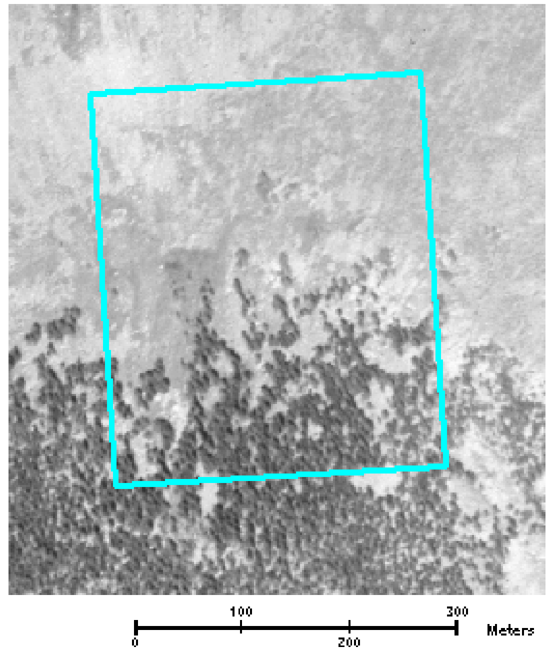
Table 5.4: Pattern metric values for each cluster centroid. Values highlighted in blue and red are, respectively, the lowest and highest pattern metric scores among the cluster centers. Also note the count for each ATE type and the within cluster sum of squares values, which is indicative of the relative compaction of each cluster. Notable acronyms include Area Weighted Mean (AWM) and Coefficient of Variation (CV)

Class	Pattern Description	Interpretation
1	ATE class 1 contains relatively few patches that are coarse in size and simple in shape. This class is dominated by herbaceous landcover and possesses very little bare rock. Landscape composition contributes heavily to the lowest contrast weighted edge density value among the clusters.	ATE samples falling in this class are predominately climatically controlled. Typical treelines in this class are characterized by small, isolated trees and/or tree patches found in areas of alpine tundra. Trees found upslope are likely to benefit from localized, topographically advantageous conditions (e.g., small rock outcrops).
2	ATE class 2 contains the fewest landcover patches. These patches tend to be coarse and have complex shapes that are consistently complex for the entire sample. Due to the shape complexity (i.e., a high proportion of cells on patch edges), this ATE class has the lowest amount of core area, despite the typically coarse patch sizes. This class also contains the highest proportion of tree cover.	These ATE samples include treelines with few (or no) trees found above the edge of the subalpine forest. As such, ATE samples in this class tend to be spatially compact. These treelines transition from trees to herbaceous landcover before (possibly) transitioning again to bare rock. The transition is typically abrupt, and the boundary between trees and herbaceous landcover is complex without being patchy (i.e., the forest edge is jagged, but contiguous).
3	ATE class 3 contains the least complex patch shapes among the classes, has the highest contagion score (i.e., the least disaggregated landscape), the highest proportion of bare ground, and the lowest proportion of tree and herbaceous cover.	The interpretation for this ATE class varies geographically as it represents (1) compact, structurally constrained treelines in all sites, but also (2) climatic treelines in areas of the southwestern U.S. (e.g., Sequoia NP) with little herbaceous landcover. Structurally controlled treelines falling into this class tend to have abrupt, smooth edges, with trees transitioning directly to bare rock. Climatic treelines falling into this class look essentially the same when viewed on remotely sensed imagery.
4	ATE class 4 has the most variable patch extent, and samples include one or more coarse, simple shaped patch(es) that possesses a coarse amount of core area. This class also has a high proportion of herbaceous landcover, with some bare ground, and relatively few trees.	This relatively unusual ATE class contains very wide treelines most commonly associated with disturbed areas, in particular snow avalanche paths. However, this class may also be associated with broad areas of relatively low relief, often possessing hummocky topography (e.g., hanging glacial valleys containing alpine lakes and wetlands). The high degree of patch size and shape variability in this class is indicative of many localized topographic controls coinciding in one belt-transect.

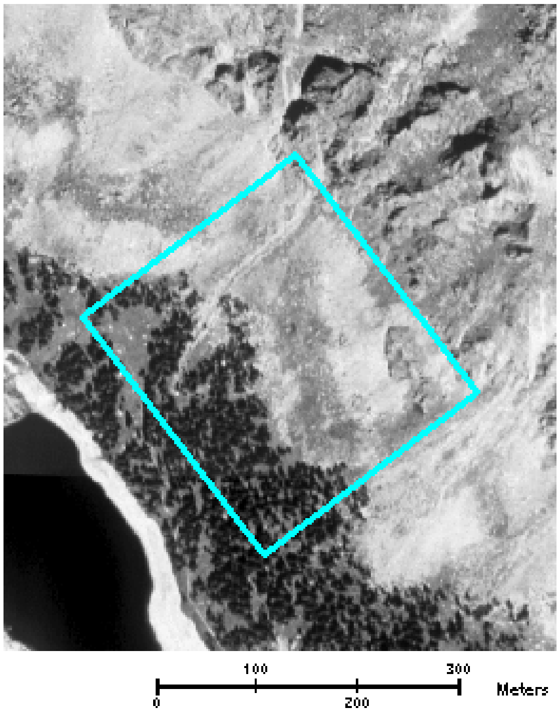
5	ATE class 5 has the most variable patch shape and is the least aggregated class. This class contains all three landcover types and has the second highest patch density.	This ATE class represents very patchy and fragmented ecotones that are climatically controlled, but affected significantly by localized structural controls. These structural controls contribute to both tree-free areas within the subalpine forest (e.g., meadows) and provide many topographically advantageous sites for tree establishment upslope. ATE samples from this class may be indicative of treelines that are advancing upslope and will eventually experience tree infilling to become sub-alpine forests.
6	ATE class 6 is the patchiest treeline type, with the smallest patches, the highest proportion of tree cover, little herbaceous cover, and the highest contrast weighted edge density. Patches in this class tend to have simple shapes and are disaggregated.	The interpretation for this ATE class is geographically variable as it represents (1) structural treelines (e.g., those limited by sheer cliffs) with isolated trees occurring further upslope in topographically conducive areas, such as ledges, or (2) patchy climatic ecotones (similar to class 5) in areas lacking abundant herbaceous landcover, such as the Sierra Nevada Mountains.

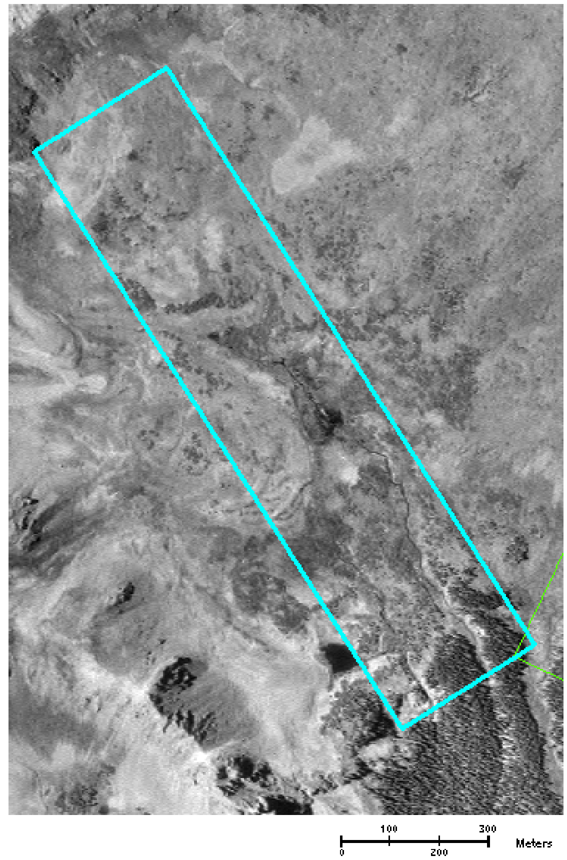
Table 5.5: Qualitative descriptions of the ATE class with respect to their patterns, and an interpretation of the ATE characteristics and controls coincident with each type.



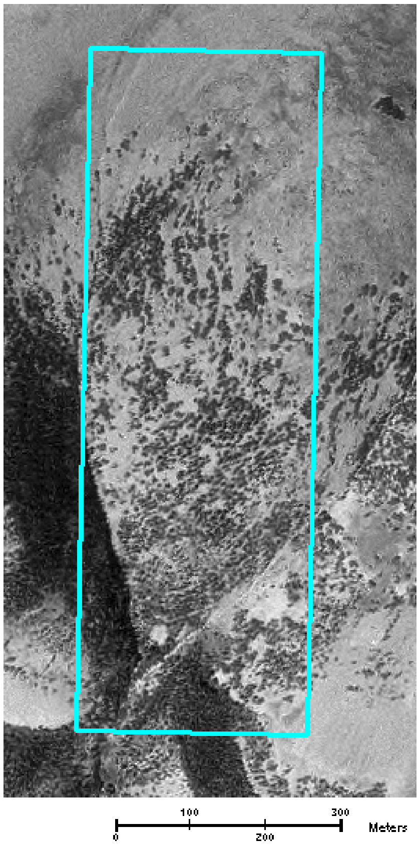


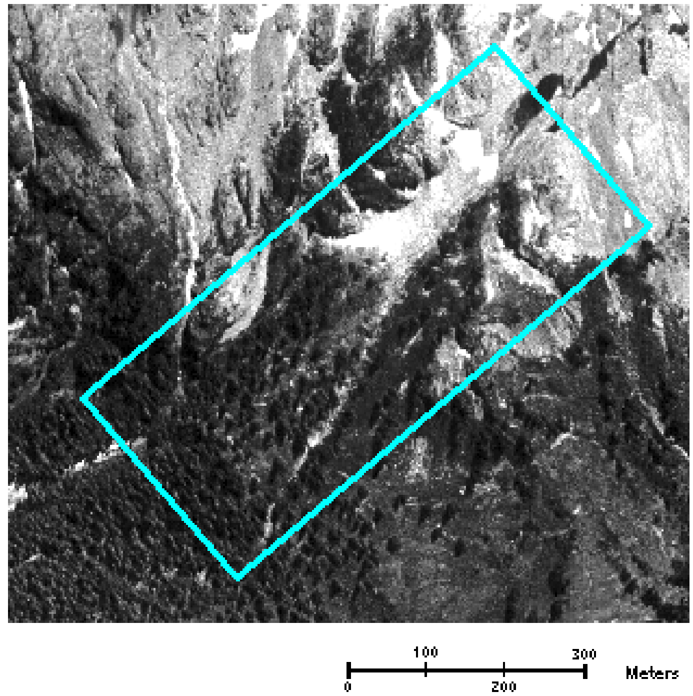
Figures 5.4 and 5.5: ATE class 1 (left) and 2 (right) shown on DOQs. These types of treelines are both attributed to climatic controls, but they differ in that class 1 has isolated trees found upslope in topographically conducive areas.





Figures 5.6 and 5.7: ATE class 3 (left) and 4 (right) shown on DOQs. Class 3 is structurally controlled by steep terrain and/or unstable slope condition (e.g., talus slopes). Class 4 is characterized by long ecotones coincident with disturbed areas (e.g., avalanche paths, or wide areas of low relief at approximately the local climatic limit of tree survival).





Figures 5.8 and 5.9: ATE class 5 (left) and 6 (right) shown on DOQs. Class 5 is attributed to wide, patchy ecotones that may be in the process of upslope advance. Class 6 represents treelines that are structurally controlled, but with some available tree habitat in isolated areas (e.g., flat structural benches on an otherwise steep cliff).

The geographic distribution of the ATE classes within the five primary study sites is shown in Tables 5.6 and 5.7, and Figure 5.10. The most notable geographic trend pertains to Sequoia National Park, which has ATE sites consisting almost entirely of classes 3 and 6. These classes are special cases in which the class interpretations are different for Sequoia National Park than for the other primary study areas. Another interesting trend occurs with ATE class 4, which is primarily attributed to long ecotones affected by snow avalanches. As such, it is not surprising that class 4 is most common in the northern study sites

(Glacier, North Cascades, and Olympic National Parks) where snow avalanche paths are frequently observed within the ATE.

	Glacier NP	Rocky Mountain NP	Sequoia NP	Olympic NP	North Cascades NP	All Sites
Class 1	41	19	0	7	8	148
Class 2	20	6	5	8	0	105
Class 3	7	13	38	22	9	152
Class 4	11	5	0	12	9	68
Class 5	30	41	2	44	33	276
Class 6	22	21	22	26	18	257

Table 5.6: ATE class distribution by study site (frequency).

	Glacier NP	Rocky Mountain NP	Sequoia NP	Olympic NP	North Cascades NP	All Sites
% Class 1	31.30%	18.10%	0.00%	5.88%	10.39%	14.71%
% Class 2	15.27%	5.71%	7.46%	6.72%	0.00%	10.44%
% Class 3	5.34%	12.38%	56.72%	18.49%	11.69%	15.11%
% Class 4	8.40%	4.76%	0.00%	10.08%	11.69%	6.76%
% Class 5	22.90%	39.05%	2.99%	36.97%	42.86%	27.44%
% Class 6	16.79%	20.00%	32.84%	21.85%	23.38%	25.55%

Table 5.7: ATE class distribution by study site (percentage).

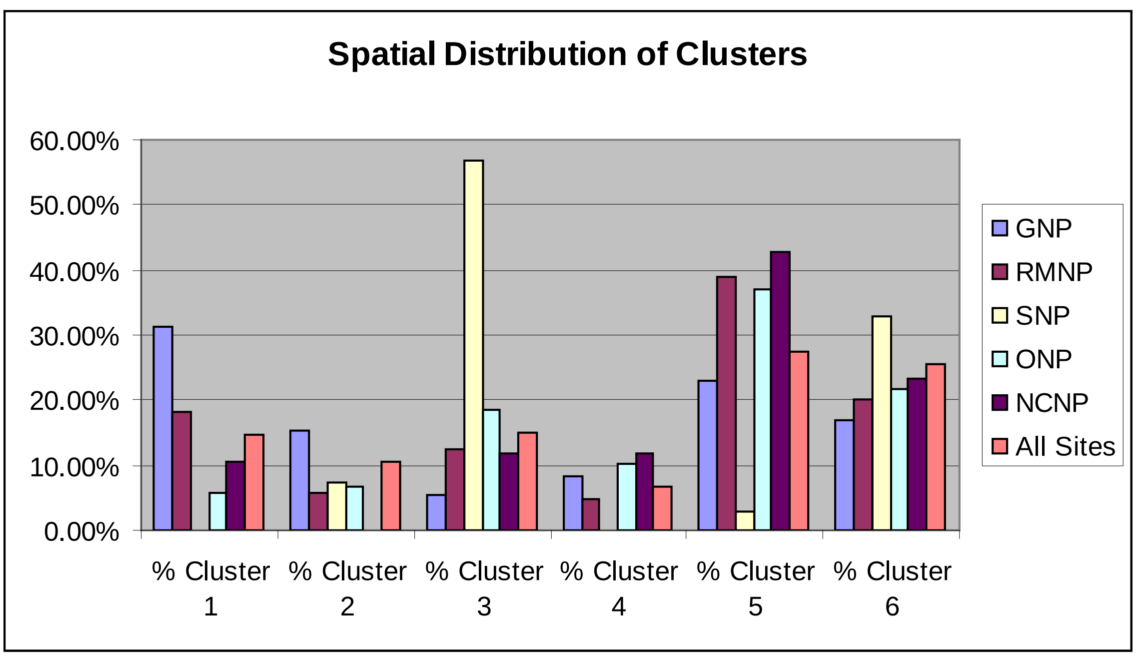


Figure 5.10: Cluster distribution by study site (percentage).

The final stages of analysis for this research consist of (1) associating environmental variables with the ATE classes, (2) assessing the geographic variability within these relationships, and (3) testing the utility of underlying topographic conditions for predicting ATE class membership. Figure 5.11 shows the relationship between each ATE class and topographic variables hypothesized to influence the ecotone. Several interesting relationships are visible within these graphs, including (1) mean slope angle is highest for class 3, which supports the interpretation that this class consists of steep, structurally controlled treelines; (2) the mean slope angle is lowest for class 4, which agrees with the interpretation that this class represents long ATE samples over which slope is averaged; (3) high measures of topographic wetness associated with class 4 support the interpretation that ATE samples in this class are coincident with snow avalanche paths, as terrain characteristics that facilitate avalanches also tend to produce streams; and (4) elevation range is effective for distinguishing the relatively wide ecotones (i.e., classes 4 and 5) from those that are spatially compact (i.e., classes 1, 2, 3, and 6). The relationship between slope aspect and the ATE pattern types is less clear, with possible exceptions including (1) class 4 has a high mean transformed slope aspect, which may suggest that snow avalanches are least prevalent on northeast facing slopes, an interpretation that makes sense as these slopes are less likely to experience mid-winter melting events; and (2) class 6 has a high mean cosine aspect, which may suggest that patchy, structurally controlled ecotones are more common on north facing slopes. Variables that showed no discernable association with ATE types include topographic roughness and all measures of slope curvature.

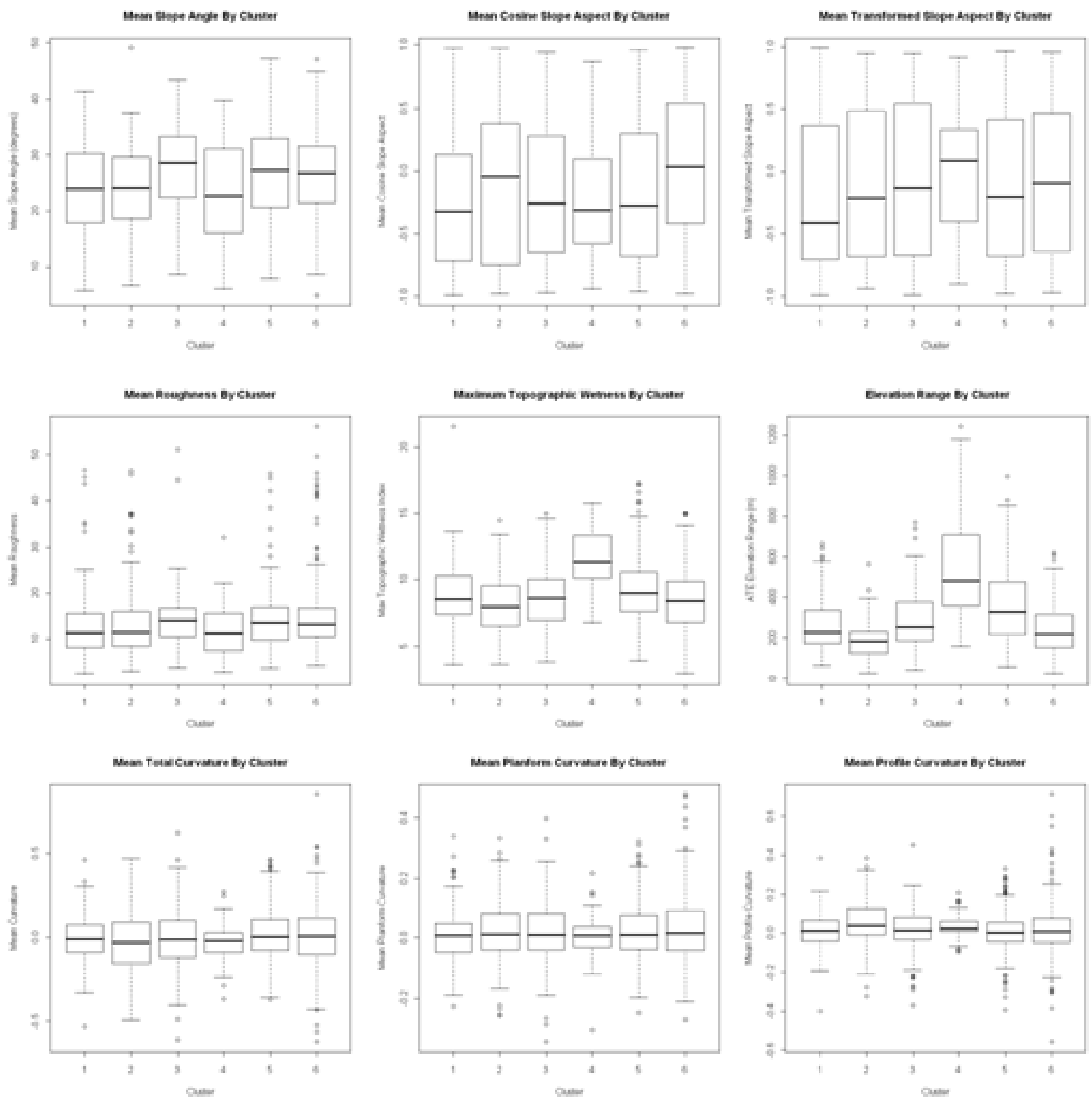
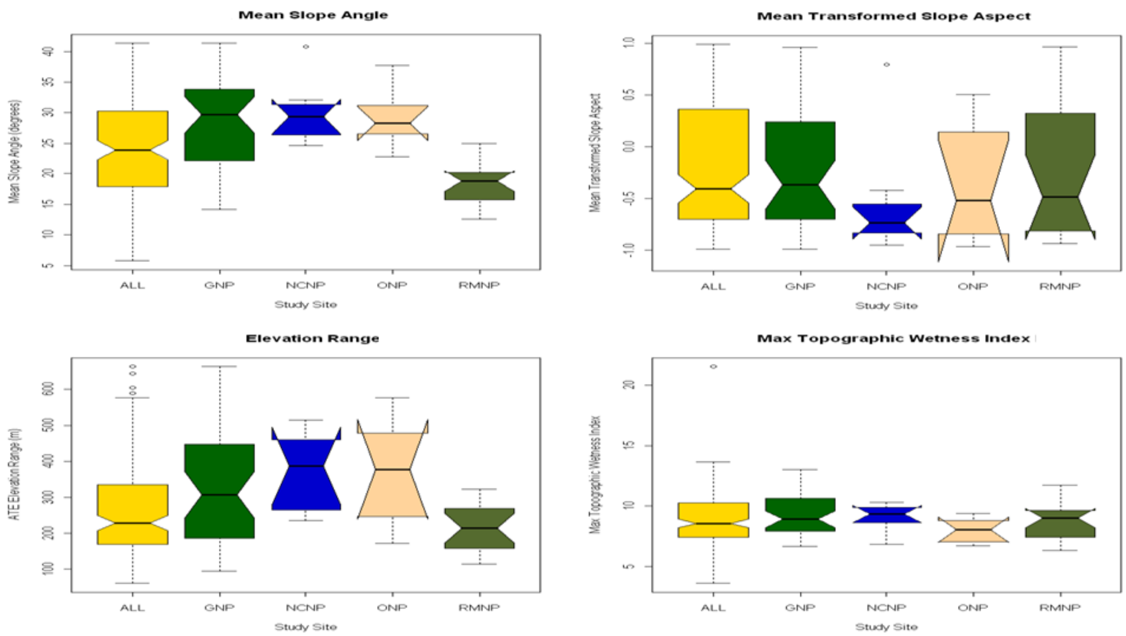


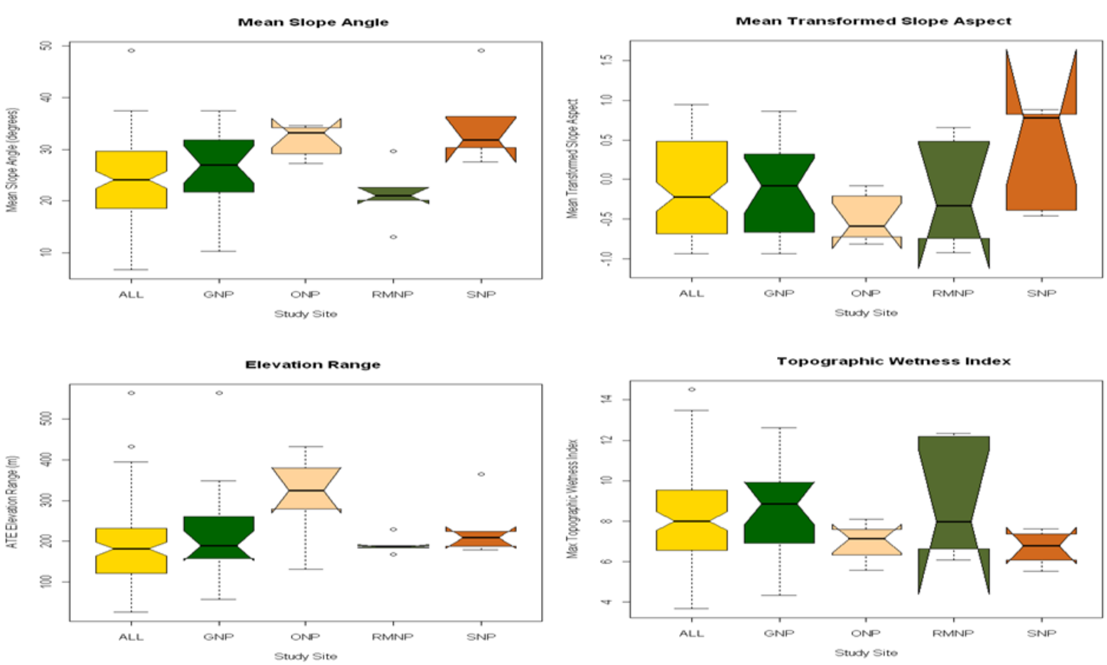
Figure 5.11: ATE classes associated with terrain characteristics.

Geographic variability in the relationship between ATE classes and topographic variables is shown in Figure 5.12. Variables selected for inclusion in this analysis are those that explained inter-cluster variability in Figure 5.11 (i.e., slope angle, transformed slope aspect, elevation range, and topographic wetness). Notched box plots are used to illustrate the differences between the sites. For reference, when comparing notched box plots, mean values from one plot falling beyond the notches (i.e., angled portions) of other box plots indicate that the datasets are significantly different. Due to geographic variability in the occurrence of ATE classes, some classes were not present or had small sample sizes at individual sites. Despite this shortcoming, some interesting geographic trends did emerge, particularly with respect to elevation range and slope angle. Elevation range tended to be highest in Olympic and North Cascades National Parks, regardless of class. Mean slope angle tended to be higher in Olympic, North Cascades, and Glacier National Parks. For Olympic and North Cascades National Parks, these two findings are related because elevation range is a product of both belt transect length and sample slope angle. Class associations for Glacier National Park, in contrast, are not consistently high in elevation range, while Rocky Mountain National Park is consistently low for both topographic variables. These findings suggest that similar patterns (i.e., pattern types) emerge in different places and despite different sets of environmental conditions; a finding further supported by classes 3 and 6 requiring unique interpretations for Sequoia National Park.

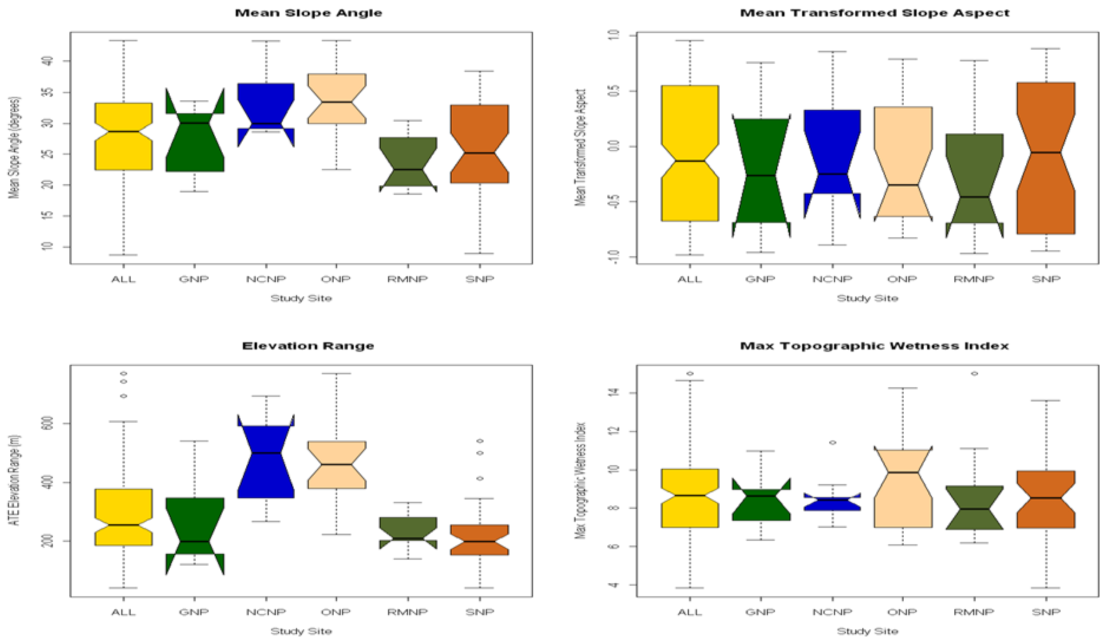
Class 1



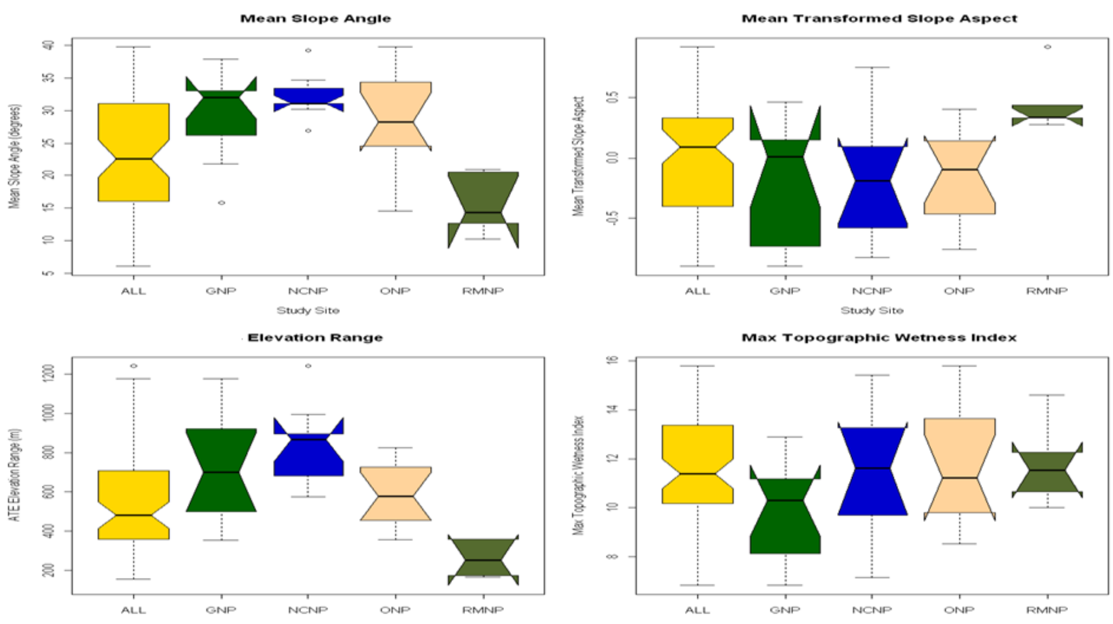
Class 2



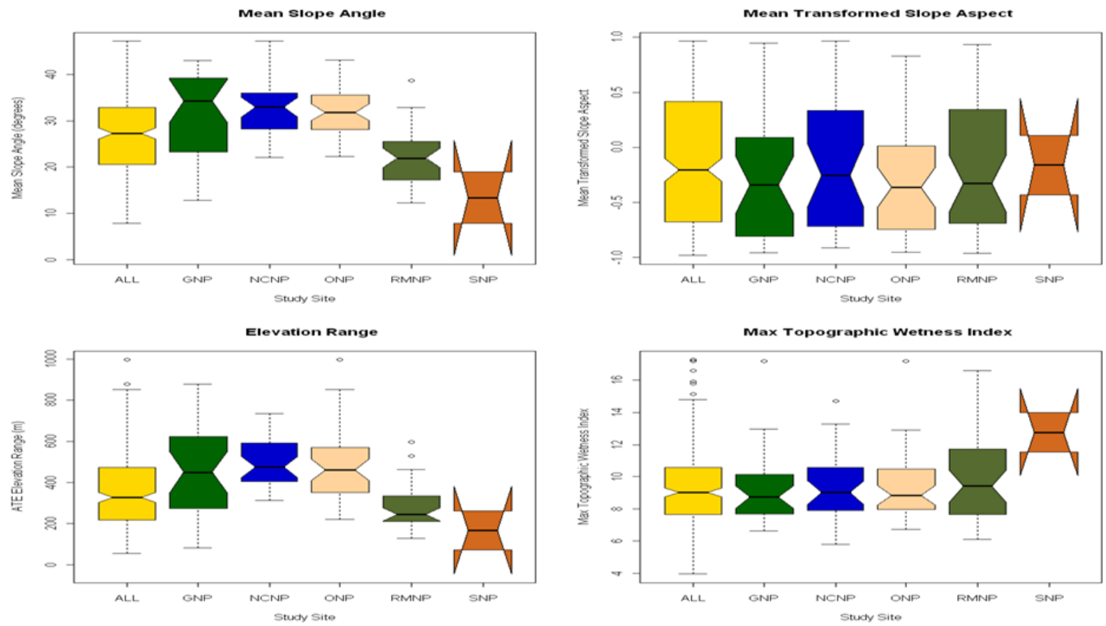
Class 3



Class 4



Class 5



Class 6

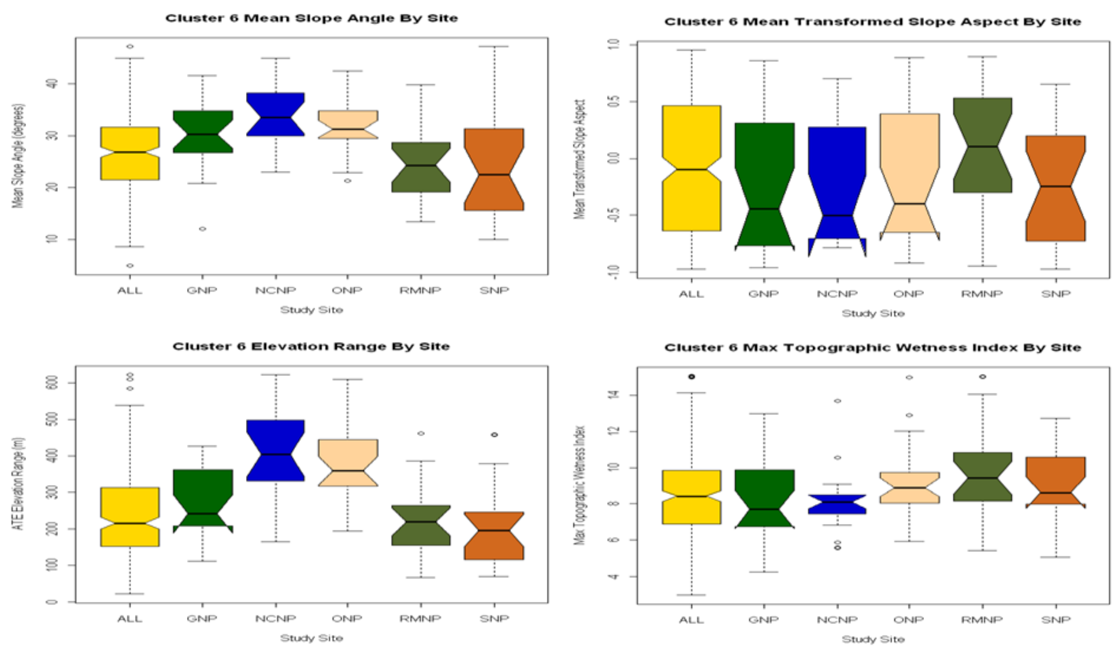


Figure 5.12: Geographic variability in the associations between ATE pattern types and environmental variables. Results for all Parks are shown in yellow, results for Glacier National Park are shown in green, results for North Cascades National Park are shown in blue, results for Olympic National Park are shown in peach, results for Rocky Mountain National Park are shown in olive, and results for Sequoia National Park are shown in orange. Note that values for all Parks are not present in all graphs as some parks had very few ATE samples classified as certain types.

To better assess the relationship between ATE pattern and topographic conditions it is necessary to move beyond simple comparisons and test these relationships statistically. CART, and specifically the classification tree, was selected for this task as it performs well with categorical data (i.e., the ATE classes). The first step when creating a classification tree was determining the optimum number of terminal nodes. For this analysis, the initial number of terminal nodes, as estimated by the v-fold cross-validation procedure, was 13 (Figure 5.13). However, this was later reduced to 11 terminal nodes through the pruning process. The final classification tree produced from the model is shown in Figure 5.14. This is the graphical representation of the tree model, including the threshold values that were used to predict ATE class membership based upon the input topographic variables. The overall accuracy of the model was only 39.96% (Table 5.8), which suggests that topographic variables alone do a relatively poor job of predicting ATE class membership. The relative importance of the topographic variables is shown in Figure 5.15, with elevation range (abbreviated DEM RNGE) proving to be the most useful for differentiation ATE pattern types generated within this analysis.

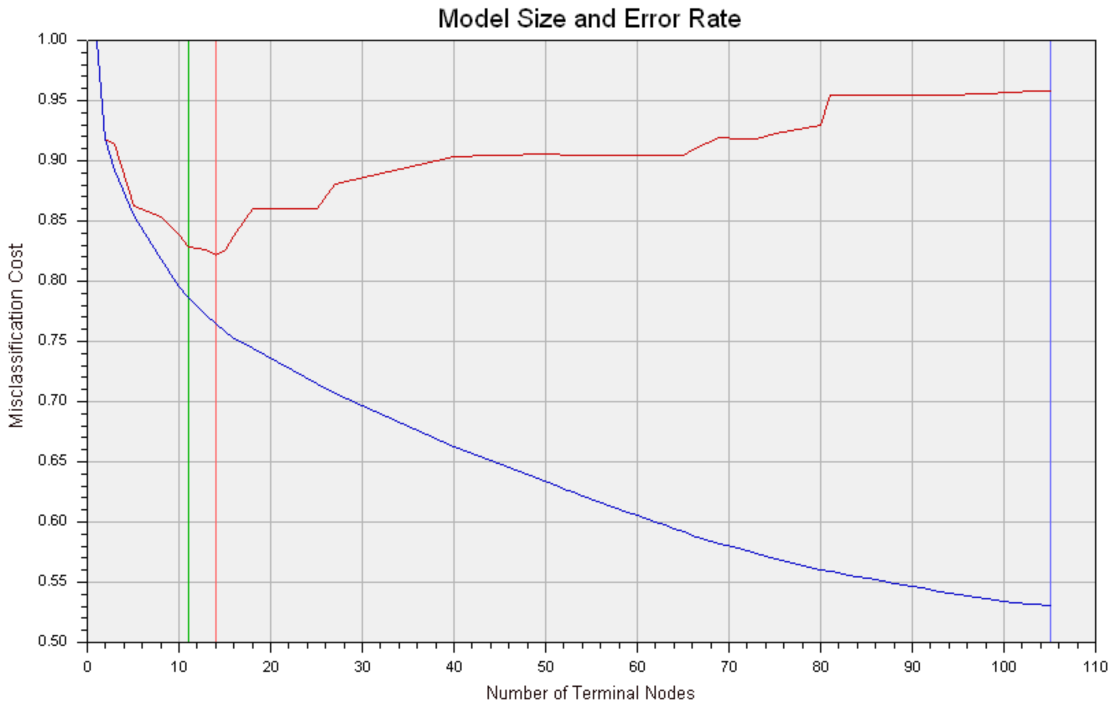


Figure 5.13: Tree size determination: the vertical red line represents the number of terminal nodes (13) indicated by a v-fold cross-validation procedure. The vertical green line represents the number of terminal nodes (11) remaining after pruning the tree.

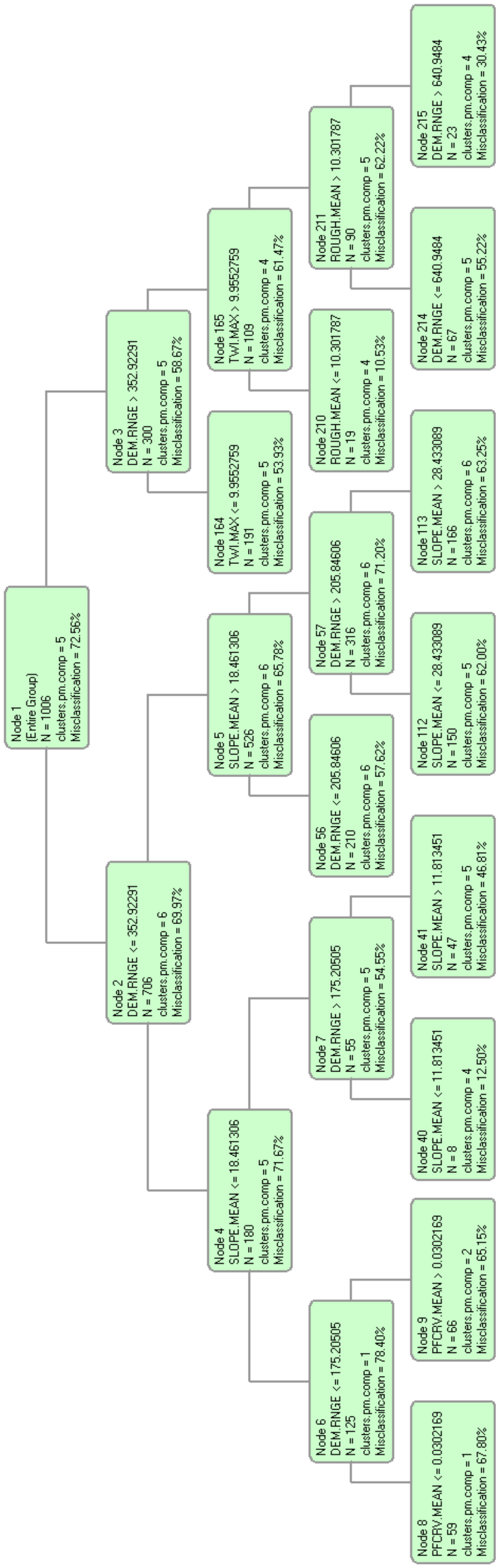


Figure 5.14: The classification tree produced to predict ATE pattern type based upon topographic variables. Note that elevation range is listed as "DEM_RNGE", maximum topographic wetness index is abbreviated TWI_MAX, mean profile curvature is abbreviated PFCRV_MEAN, and mean roughness is abbreviated ROUGH_MEAN.

Class	Actual Count	Misclassified Count	Percent Misclassified	Percent Correctly Classified
1	148	136	91.89%	8.11%
2	105	86	81.91%	18.10%
3	152	152	100.00%	0.00%
4	68	37	54.41%	45.59%
5	276	81	29.35%	70.65%
6	257	112	43.58%	56.42%
Total	1006	604	60.04%	39.96%

Table 5.8: The accuracy for the classification tree for predicting ATE pattern type using topographic conditions.

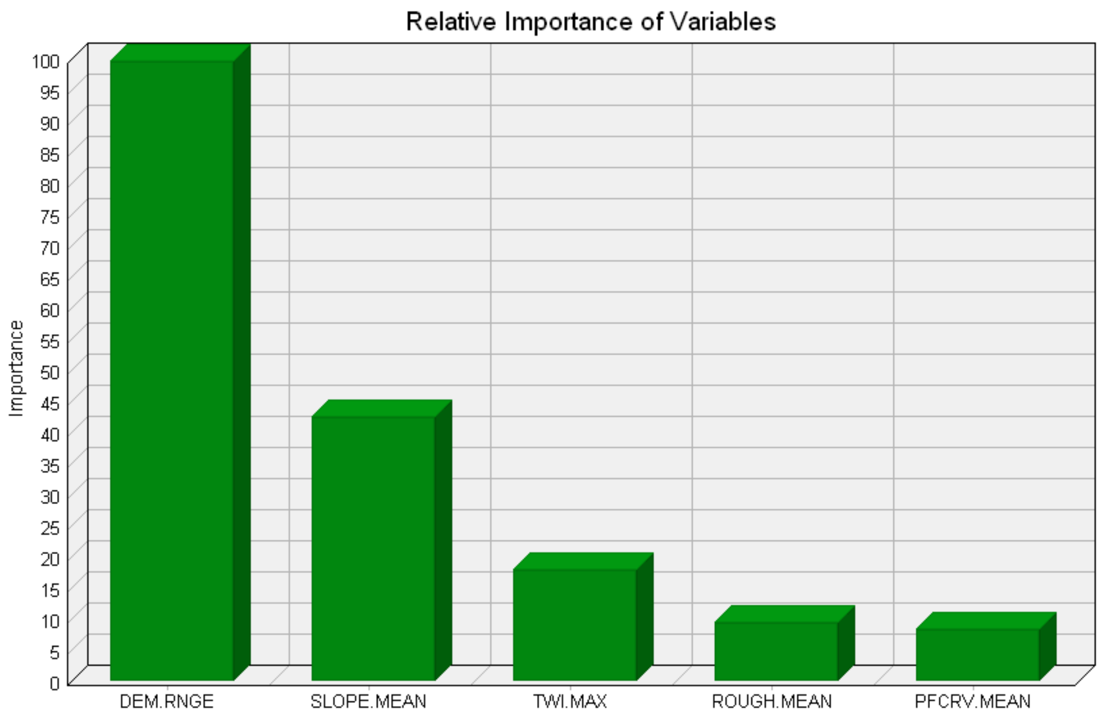


Figure 5.15: The relative importance of variables used within the classification tree.

Two additional tests were conducted (results not shown) to test the predictive capabilities of non-topographic variables. The first classification tree included study area as a categorical predictive variable, in addition to all the topographic variables used in the classification tree described above. The second test further expanded the set of predictive variables to include climatic conditions (i.e., summary statistics for annual temperature, incident shortwave radiation, and precipitation), and geographic information (i.e., latitude and longitude). Despite the additional variables, the predictive capability of these trees was improved only slightly (i.e., accuracies of 42.44% and 44.63% respectively). However, the modest improvement in accuracy produced by these alternative classification trees was accompanied by simpler models (i.e., fewer splits and terminal nodes). The variables used to split the classification tree are also notable as mean annual precipitation and annual precipitation standard deviation were most useful for differentiating pattern types.

5.6.0 Discussion

This research represents an advance in the study of ATE pattern-process relationships by (1) defining a regional-scale ATE typology based on 2-D landcover patterns; (2) presenting an automated methodology for deriving ATE pattern types for multiple study areas; and (3) examining geographic variability in the relationships between ATE pattern types and environmental variables hypothesized to influence the ecotone. The definition and interpretation of an ATE typology, generated though cluster analysis, was based largely on the simple ATE typology defined by Holtmeier (2003) (i.e., treelines are classified as climatically- or orographically-controlled based on the conditions that prevent them from advancing upslope). This research extends Holtmeier's typology, however, by incorporating fine scale spatial variability in ATE patterns within the analysis to further specify the localized processes and conditions responsible for patterns visible in the ecotone. For example, treelines predominantly limited by climatic conditions may contain isolated areas of orographically-controlled treelines and vice-versa. Incorporation of fine scale pattern-process relationships is accomplished by fusing Holtmeier's typology with research findings that link localized ATE patterns to topographic controls, particularly as they pertain to moisture (e.g., Bunn et al. 2005b, e.g., Rochefort and Peterson 1996). The resulting treeline typology effectively expands Holtmeier's typology to better match complex treelines seen in nature.

The methodological advances presented in this chapter expand upon the techniques used by Allen and Walsh (1996) and Baker and Weisberg (1995) to explore ATE landcover patterns by increasing the geographic scope of analysis from individual National Parks to the entire region. The challenge inherent to this research was to capture ATE pattern at a fine spatial scale, but to analyze this information at a broad spatial scale. Broad spatial scale analysis essentially consisted of comparing and contrasting ATE patterns and topographic variables hypothesized to influence these patterns, for study areas distributed across the western U.S. This research necessitated a methodological approach that was simultaneously able to capture detailed information about ATE patterns, while being generalizable and consistent across the entire region. The fundamental input data source for the pattern analysis was Landsat imagery, which was selected for its availability at all study sites, and was classified to identify a regionally-consistent set of landcover classes. The classification scheme utilized in this research consisted of basic landcover types (i.e., bare rock, conifer trees, herbaceous vegetation, and water), which are applicable to analyses conducted at coarser and finer spatial scales. The methodological approach, therefore, is very flexible and can easily be modified to incorporate higher resolution satellite imagery in an effort to capture patterns at finer spatial scales.

Pattern-process analyses were conducted for this research at the regional scale and for individual study sites by associating defined ATE pattern types with environmental variables hypothesized to influence the ecotone. The set of environmental variables used in this analysis was limited to topographic variables including slope angle, slope aspect, slope curvature, topographic roughness, and topographic wetness, because (1) these variables are hypothesized to be among the most significant drivers of ATE pattern at the scale of the belt transect samples, and (2) these variables were simple to calculate for all study sites using readily available data sets. This approach, however, did not include datasets that quantify all processes and conditions known to influence ATE patterns. Foremost among these influences on ATE pattern are feedback effects, ATE species composition, and underlying geologic conditions. Feedback effects within the ATE have been researched, for example, by Alftine and Malanson (2004), Bekker (2005) Germino et al. (2002), and Wilson and Agnew (1992) who all explored important sheltering effects produced by existing vegetation that benefit seedlings within the ATE. Feedback processes within the ATE, therefore, may simultaneously be considered the product of previous vegetation patterns and a cause of future patterns. Although feedback processes related to ATE vegetation are not included within this analytical framework, sheltering effects from topography are somewhat encapsulated by measures like topographic roughness, which influences the redistribution of snow within the ATE (Hiemstra et al. 2002).

ATE species compositional differences are likely to contribute to geographic variability in ATE pattern due to (1) different life strategies of the tree species, and (2) the type and density of herbaceous cover present within the ecotone. Among the primary study areas analyzed in this research, ATE species characteristics were comparable for 4 out of 5 study areas, with the exception being Sequoia National Park. Key features differentiating ATE sites in Sequoia National Park from those in other primary study areas include (1) the prevalence of foxtail pine (*Pinus balfouriana*) which, unlike ATE tree species common in other parts of the western U.S., tends to grow as tall, isolated individual trees rather than in dense tree patches that can take advantage of localized habitat improvements gained through feedbacks; and (2) the relatively sparse herbaceous cover present in the southern Sierra Nevada Mountains. The net effect of these features is an ATE characterized by transitions from conifer trees directly to bare rock, and generally patchier ecotones as each tree can be considered a patch.

Geologic conditions are pertinent to ATE vegetation patterns because rocks resistant to erosive processes (e.g., granite) tend to provide a more stable base upon which soils can develop and trees can establish. In contrast, less resistant rock (e.g., shales and mudstones) are more susceptible to mechanical weathering (i.e., freeze-thaw processes) and more prone to mass movements such as slumping and sliding. For ATE trees, these processes are effectively geomorphic disturbances that may affect ATE landcover patterns (Butler and Walsh 1994). The influences of different geologic conditions may be evident within the results from this research as the three northern study areas (i.e., GNP, ONP, NCNP), which frequently had ATE areas coincident with sedimentary rocks, tended to have similar ATE landcover patterns (Figure 5.12). In contrast, the two southern sites (i.e., SNP and RMNP) are both dominated by granite, and tended have similar relationships between ATE pattern and topographic settings. However, this observation may simply be indicative of regional scale temperature and/or precipitation gradients that also differentiate the southern and northern study areas.

Important limitations of the analytical approach used in this Chapter are (1) that the derived ATE patterns represent only single snapshots of a dynamic ecological phenomenon, and (2) that the analysis of pattern was restricted to a single spatial scale (i.e., it was based only on 30-meter spatial resolution Landsat imagery). The first limitation is notable as treelines, like all ecotones, frequently move and change in response to changing climatic conditions. In fact, changes in ATE characteristics (i.e., tree infilling or upslope advance) are an often explored topic in the literature (e.g., Kullman 1998) as they may provide evidence for environmental changes (i.e., climate change or changes in human land-use patterns). Longitudinal analyses of ATE change, however, are impractical at the scale of the region because (1) historical reconstructions of treeline conditions are labor intensive and realistic only for fine scale analyses; (2) limited data are available for historical treeline analyses, as remotely sensed imagery archives are too shallow to effectively capture the slow and subtle changes typical at the ATE; and (3) the datasets available for assessing former ATE conditions (i.e., terrestrial photos) are not consistent for all sites, which violates an intent of this research (i.e., maintaining a standardized analytical framework). The second limitation is important because landscape patterns are scale-dependent phenomena. As such, the results from identical analyses conducted using imagery with different spatial resolutions would be different. Future research exploring ATE patterns, therefore, may benefit from analyzing pattern derived at multiple spatial scales, but such endeavors are likely to face the challenge of finding and/or creating adequate independent variables at comparable resolutions. Despite these notable limitations, the analysis conducted in this Chapter has utility because (1) treelines experiencing changes are still affected by the underlying physical template of the landscape, and (2) an analysis at a single scale still produced interpretable, albeit scale-dependent results.

Relationships between ATE pattern types and environmental variables hypothesized to influence the ecotone were explored using a combination of simple descriptive statistics, which were used to compare and contrast primary study sites, and classification trees, which were used to test the predictability of ATE patterns based solely on underlying topographic conditions. The hypothesis underlying these analyses is that 2-D ATE landcover patterns result, in part, from the underlying structure of the landscape. Results from these analyses, however, do not support this hypothesis as ATE landcover patterns derived from classified Landsat imagery, and summarized at the scale of the belt transect samples, are not strongly related to topographic variables derived from DEMs. Despite this finding, there were some notable relationships between ATE pattern types and topographic variables, such as mean elevation range and maximum topographic wetness values, which were all significantly higher for ATE class 4 (i.e., the landcover pattern class associated with snow avalanche paths).

Another intent of this research was to assess whether ATE patterns are polygenic in nature (i.e., if similar patterns occur despite different underlying processes). Interpretation of the ATE pattern typology seems to support this idea as two classes (i.e., class 3 and class 6) appear to have a geographically variable interpretation due to characteristics of the ATE in the Sierra Nevada Mountains. Additional support for the concept of polygenic patterns is provided by the box-plots in Figure 5.12, which show that the topographic conditions coincident with ATE pattern types are geographically variable.

As with the descriptive statistics, results from the classification tree analysis do not show clear relationships between ATE pattern types and topographic effects. There are several likely explanations for the poor performance of the classification tree and for the descriptive statistics discussed above. Most notable among these explanations are (1) the coarse resolutions of the Landsat imagery and the DEM layers relative to ATE landcover patches and topographic features, respectively; (2) the loss of detail that occurred when patterns and topographic variables were summarized at the scale of the belt transect; and (3) the omission of potentially important environmental covariates affecting ATE pattern from this analysis. These shortcomings can all be attributed to the research requirement of maintaining a consistent analytical framework for all study sites. Fortunately, the input datasets and the analytical framework developed for this research can be easily modified to incorporate new information if/when better datasets become available. Therefore, this research can be viewed as a first attempt to quantify and explain ATE pattern similarities and differences across the western U.S., rather than the end of a research agenda. One notable avenue for potential future research would be to include 3-D tree and tree patch characteristics in the pattern creations process to better match *in situ* assessments of variables influencing ATE character.

5.7.0 Conclusion

The research presented in this Chapter contains several interesting findings including (1) the emergence of an interpretable ATE typology that effectively categorized ATE samples according to the processes responsible for producing ecotone patterns across a large and diverse geographic region; (2) the identification of important geographic differences in the production of ATE patterns, most notably the uniqueness of ATE samples in Sequoia National Park relative to other primary study areas used in these analyses; (3) the generally poor association between topographic variables and ATE pattern, which is attributed primarily to the limitations inherent to the input datasets; and (4) some evidence that ATE patterns are polygenic in nature. The ATE typology and the geographically variable associations between ATE types and environmental controls also provide contextual information for past and future ATE research conducted within the western United States.

5.8.0 References

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

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

Bader, M. Y., M. Rietkerk, and A. K. Bregt. 2007. Vegetation structure and temperature regimes of tropical alpine treelines. *Arctic Antarctic and Alpine Research* 39: 353-364.

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

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

Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Aspect transformation in site productivity research. *Journal of Forestry* 691–692.

Bekker, M. F. 2005. Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, U.S.A. *Arctic, Antarctic, and Alpine Research* 37: 97-107.

Billings, W. D., and L. C. Bliss. 1959. An alpine snowbank environment and its effects on vegetation, plant development, and productivity. *Ecology* 40: 388 - 397.

Breiman, L., J. Friedman, C. J. Stone, and R. A. Olshen. 1984. *Classification and regression trees*. Chapman & Hall, New York, N.Y.

Brown, D. G. 1994. Predicting vegetation types at treeline using topography and biophysical disturbance variables. *Journal of Vegetation Science* 5: 641-656.

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

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

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

Butler, D. R., and S. J. Walsh. 1990. Lithologic, structural, and topographic influences on snow-avalanche path location, eastern Glacier National Park, Montana. *Annals of the Association of American Geographers* 80: 362-378.

—. 1994. Site characteristics of debris flows and their relationship to alpine treeline. *Physical Geography* 15: 181-199.

Daniels, L. D., and T. T. Veblen. 2003. Regional and local effects of disturbance and climate on altitudinal treelines in northern Patagonia. *Journal of Vegetation Science* 14: 733-742.

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

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

Holtmeier, F. K. 2003. *Mountain Timberlines: Ecology, Patchiness, and Dynamics*. Springer, Berlin.

Holtmeier, F. K., and G. Broll. 1992. The Influence of Tree Islands and Microtopography on Pedoecological Conditions in the Forest Alpine Tundra Ecotone on Niwot Ridge, Colorado Front Range, USA. *Arctic and Alpine Research* 24: 216-228.

Kullman, L. 1998. Tree-limits and montane forests in the Swedish Scandes: Sensitive biomonitors of climate change and variability. *Ambio* 27: 312-321.

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

Malanson, G. P. 2001. Complex responses to global change at alpine treeline. *Physical Geography* 22: 333-342.

McGarigal, K., and B. J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. *USDA Forest Service General Technical Report PNW-351*.

O'Neill, R. V., J. R. Krummel, R. H. Gardner, G. Sugihara, B. Jackson, D. L. DeAngelist, B. T. Milne, M. G. Turner, B. Zygmunt, S. W. Christensen, V. h. Dale, and R. L. Graham. 1988. Indices of landscape pattern. *Landscape Ecology* 1: 153 - 162.

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

Riaño, D., E. Chuvieco, J. Salas, and I. Aguado. 2003. Assessment of different topographic corrections in Landsat-TM data for mapping vegetation types. *IEEE Transactions on Geoscience and Remote Sensing* 41: 1056 - 1061.

Riitters, K. H., R. V. O'Neill, C. T. Hunsaker, J. D. Wickham, D. H. Yankee, S. P. Timmins, K. B. Jones, and B. L. Jackson. 1995. A factor analysis of landscape pattern and structure metrics. *Landscape Ecology* 10: 23 - 29.

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

Teillet, P. M., B. Guindon, and D. G. Goodenough. 1982. On the slope-aspect correction of multispectral scanned data. *Canadian Journal of Remote Sensing* 8: 84 - 106.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* 20: 171-197.

Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385 - 397.

Wilson, B. A., and S. E. Franklin. 1992. Characterization of alpine vegetation cover using satellite remote sensing in the Front Ranges, St. Elias Mountains, Yukon Territory. *Global Ecology and Biogeography Letters* 2: 90-95.

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

Chapter 6

CONCLUSIONS AND SYNTHESIS

6.1.0 Introduction

The results presented in this dissertation provide new insights into the dynamics of the Alpine Treeline Ecotone (ATE) in the western United States. The fundamental motivation for this research was to provide an empirical foundation to support and describe scale-dependent relationships between ATE characteristics and hypothesized environmental controls. To help explain these relationships, statistical methods were used to quantify the relationships between ATE characteristics (i.e., elevation, tree presence, and landcover pattern) and a set of environmental covariates including climatic and topographic variables. What makes this research particularly unique is the regional scope of the analysis, which facilitates the exploration of geographic variability and scale-dependencies inherent within ATE pattern-process dynamics. The findings from this research provide a regional context into which site-specific ATE findings can be assessed and compared, as well as several standardized analytical frameworks that can be extended to address future research questions in the western U.S. and elsewhere.

6.2.0 Chapter Summaries

Chapter 2 compares and contrasts ATE characteristics for five National Park study areas using field-based measures of vegetation features and topographic settings. Notable findings from this Chapter support field observations noted in the literature and include (1) the association between ATE elevation and latitude; (2) the identification of geographic differences present in relationships between ATE characteristics and coincident abiotic conditions, in particular the variable nature of the influence of microtopographic features on the ATE; (3) evidence for increased ATE variability in areas with frequent disturbances; (4) documenting the influence of species composition on ATE tree height and patch size; (5) describing geographic differences in the proportions of ATE landcover types that reflect the prevalence of structurally controlled treelines; and (6) demonstrating the association between ATE growth form and elevation. A second analysis in Chapter 2 explored the utility of digital datasets for ATE analyses. Data types explored include Digital Elevation Models (DEM) and remotely sensed imagery, which are both commonly applied in ATE analyses that quantify ecotone characteristics. Results from this analysis suggest that these datasets generally do a poor job of capturing microtopographic features and fine scale vegetation patterns of interest to ATE researchers. In contrast, measures of topographic features that capture more generalized slope conditions, such as slope angle and slope aspect, tend to be more accurate and are judged to retain utility in ATE analyses.

Chapter 3 provides an empirical test of the scale-dependant relationships between ATE elevation and hypothesized environmental controls described by Holtmeier and Broll (2005) and others. Important findings include (1) strong correlations between climatic controls and ATE elevation at coarse spatial scales, (2) weaker correlations between topographic controls and ATE elevation at fine spatial scales, and (3) the non-significant relationship between species composition and ATE elevation after controlling for the influence of other environmental factors and geographic distance. A noteworthy relationship was identified at the regional scale between mean annual shortwave radiation and ATE elevation. This finding is indicative of the relationship between ATE elevation and temperature that frequently is the focal point of ATE-environment research (e.g., Körner and Paulsen 2004). Mean annual precipitation was significantly correlated with ATE elevation at the regional scale. As with shortwave radiation, the strength of the correlation between precipitation and ATE elevation decreases at finer spatial scales, but this relationship reintensifies at scales of about 300 km, a finding that is attributable to rain shadow effects. All topographic variables (i.e., elevation range, slope angle, slope aspect, and slope curvature) had significant correlations with ATE elevation, but these correlations were consistently weaker than those found between ATE elevation and climatic effects. This finding is most likely a product of (1) geographic variability in the strength of relationships between topographic variables and ATE elevation, and (2) the spatial scale of the source dataset for the topographic variables (i.e., DEMs) relative to the size of microtopographic features hypothesized to affect the ecotone.

Chapter 4 focuses on assessing geographic variability in relationships between tree presence within the ATE and topographic covariates. Notable findings from this Chapter include (1) the consistent, and strongly significant, relationship between ATE tree presence and elevation, and (2) the lack of consistency in the relationship between ATE tree presence and any other environmental covariates included in the model. Among the covariates other than elevation, measures of slope aspect (i.e., cosine, sine, and transformed) were the variables most frequently associated with ATE tree presence, but the specific slope aspect measure and the associated regression parameters varied geographically. At finer spatial scales, the geographic variability in these relationships continued to be evident, with notable results including east-to-west and altitudinal trends (i.e., coincident with climatic gradients occurring at multiple spatial scales) in the strength of the relationship between elevation and tree presence.

Chapter 5 analyzes regional variability in ATE patterns and associations between these patterns and environmental conditions. ATE landcover patterns are of interest because they are indicative of the fundamental environmental conditions constraining the ecotone (i.e., factors preventing treelines from advancing upslope to higher elevations) (Holtmeier 2003). An important result from this Chapter is the 6-class, ATE pattern typology that is applicable for the entire region, despite the diversity of ATE areas found in the western U.S. The ATE typology was interpreted within the context of established ATE theory, and the resulting interpretations suggest that the typology captures features that can distinguish the fundamental controls acting on the ecotone. Quantifying relationships between ATE types and environmental variables, however, was less successful. Possible reasons for this result include (1) the topographic variables selected to capture features relevant to ATE pattern failed to do so, and/or (2) the scale mismatch between the datasets used to derive ATE landcover pattern, and spatially-coincident topographic variables, precluded strong statistical relationships.

6.3.0 Synthesis - Contributions to ATE Research

Results from this dissertation generally agree with previous research findings detailing environmental controls acting upon ATE characteristics. Evidence for such support is provided by field-based findings reported in Chapter 2, and in results from statistical analyses reported in Chapters 3, 4, and 5. Findings from this research also support the hypothesized scale-dependent nature of ATE controls described by Holtmeier and Broll (2005) and Seastedt et al. (2004). In particular, the results indicate that regional scale ATE variability is primarily the result of climatic conditions. Among climatic variables, mean annual incident shortwave radiation (i.e., a surrogate variable for temperature) showed the strongest relationship with ATE elevation, but mean annual precipitation was nearly as important and also displayed geographically variable influences at sub-regional scales. At finer spatial scales, the importance of temperature was again affirmed by the strength of the relationship between tree presence and elevation for all study areas. The other topographic variables included in this analysis, in contrast, had consistently weaker relationships with ATE characteristics (i.e., tree presence and landcover patterns), even at fine scales of analysis. This finding is most likely an indication of (1) methodological and/or source data limitations, and (2) the complex and highly variable nature of relationships between ATE characteristics and localized slope conditions. Lastly, ATE landcover patterns were associated with tree species composition, but changes in tree species composition were not significantly related to changes in treeline elevation after controlling for geographic space. This suggests that the combined physiological constraints on the growth of the trees (e.g., their tolerances for cold temperatures) inhabiting the ATE at regionally distributed sites, are fairly similar, or at least similar enough to preclude a statistically significant response.

The second important contribution to ATE research provided by this dissertation is contextual information useful for interpreting site-specific ATE research results relative to other treelines in the western U.S. Specific examples include (1) the relative importance of distance between sites as it relates to climatic variability (e.g., the approximate spatial range at which sites can be considered climatically the same with respect to ATE dynamics); (2) identification of geographically variable relationships between ATE characteristics and abiotic conditions; (3) the failure to identify any topographic variables other than elevation that were significantly related to tree presence at more than two study sites; and (4) quantifiable, empirically based distinctions between ATE pattern types, plus descriptions of the associations between patterns, abiotic conditions, and species composition.

The final contribution to the field of ATE research provided by this dissertation is as a direct assessment of the limitations of commonly used datasets. The most noteworthy finding is the judgment that existing DEMs are inadequate for analyses of fine scale ATE pattern-process relationships. Additional assessments relate to the strengths and weaknesses of modeled climate data (i.e., DAYMET), species range maps (Little 1971), and remotely sensed imagery (i.e., Landsat). In all cases, these datasets represent either the best available data of their kind and/or the most cost effective data source given the ambitious geographic scope of this research. All data sources, however, suffered from limitations imposed by their spatial resolutions and, as a result, the level of detail contained within research findings is similarly limited. Barring significant investments directed toward creating improved datasets, these limitations are likely to typify regional scale ATE analyses. Site-specific ATE research, however, can and should incorporate better datasets when and where they are available.

6.3.1 Synthesis –Connections to General Ecotone Research

This research goes beyond analyses typically applied to ecotones by directly exploring regional scale geographic variability in *relationships* between vegetation characteristics and the abiotic conditions. In doing so, this research highlights the complex nature of ecotones, which simultaneously share common traits and respond to the same fundamental climatic controls, and yet display tremendous fine scale variability in both character and pattern-process relationships. In other words, regional-to-global scale controls and unique local circumstances combine to produce ecotones, and research limited to only broad or fine scales will invariably miss important influences. Furthermore, effectively predicting future states of ecotones, a highly desirable research outcome given ongoing and prospective climate change, will require detailed understanding of ecotone influences at a wide range of spatial scales. For example, predicting how the ATE will respond to anticipated climate changes requires detailed, site-specific understandings of (1) what controls (e.g., abiotic controls, physiological limitations of plant species, and feedback mechanisms) have produced present day ecotone characteristics?; (2) if and how interactions between these controls will respond to changing climatic conditions, thereby encouraging or impeding changes within the ecotones?; and (3) what, if any, role will be played by stochastic processes?

The research presented in this dissertation fits within several established conceptual frameworks useful for interpreting and describing ecotones. For example, Gosz (1992) designed a framework that explains ecotone formation as a product of nested controls that include abiotic conditions, biotic/abiotic interactions (e.g., feedbacks), and finally biotic interactions (e.g., competition and facilitation). This research presented in this dissertation fits within the first category of Gosz's hierarchy, and therefore helps establish a foundation upon which finer scale ATE processes can be explored. The research presented within this dissertation also fits within the framework developed by Strayer et al. (2003), which focuses on the processes leading to the formation and maintenance of ecotones.

6.4.0 Future Research

The analysis presented in this dissertation represents only an initial step in the regional analysis of ATE character from which numerous potential research avenues may emerge. The most obvious progression for this research involves simply increasing the quality of the input datasets used to derive the environmental covariates, and/or using alternate statistical approaches for analyzing the data. Datasets that would add considerably to the analyses presented in this dissertation include (1) high spatial resolution DEMs (e.g., LiDAR) that more completely capture topographic variability within ATE samples, (2) high spatial resolution multi-spectral imagery that would substantially improve the level of detail available for analysis of ATE landcover patterns, (3) high spatial and temporal resolution meteorological datasets that are derived for each study area from local base-station data, and (4) additional results from fine scale ATE analyses that provide information for interpreting regional results and for generating hypotheses that are testable within the described methodological framework. Other research avenues likely to be explored include (1) expanding the geographic range of these analyses, possibly by including ATE sites in high latitude areas (i.e., in Canada and/or Alaska); (2) increasing the sampling density within the established study sites and, where possible, adding new sample areas (e.g., Mount Rainier) between the existing study sites; (3) conducting field data collection in selected secondary study sites to effectively convert them into primary study sites amenable to more detailed analyses; (4) utilizing additional data collected in the field at primary sites to characterize the 3-dimensional structure of the ATE (i.e., heights of trees and tree patches) using remotely sensed imagery, and (5) incorporating the empirical findings from this research into a spatially explicit modeling framework designed to predict future states of the ATE under various scenarios (e.g., different climate change scenarios).

6.5.0 Conclusion

This dissertation provides a description and an analysis of geographic variability of the ATE within the western U.S. The key findings from this research suggest that the ATE is a boundary that responds to abiotic conditions at multiple spatial scales. Although this assessment is not unique, previous assessments of ATE dynamics within the region (c.f., Malanson et al. 2007) have not been accompanied by quantitative, empirically derived results. Furthermore, the results from this research represent an assessment of ATE dynamics with a geographic scope atypical for most ATE research and rare for analyses of any ecotone.

Sacrifices were made to facilitate this analysis, in particular through the use of datasets with less-than-ideal spatial resolutions, but such concessions were necessary for an ATE research project that maintains consistent analytical frameworks, comparable inputs datasets, and uniform sampling designs for analyses of multiple sites. The benefits of this approach are evident in research findings that quantify ATE character and pattern-process relationships across a large and diverse geographic area. The utility of this research lies primarily in its ability to provide a regional context for interpreting detailed, fine scale ATE analyses produced within the western U.S. Future research built upon the results from this dissertation will continue to detail regional variability in ATE pattern-process relationships, as well as expand the understanding of how ATE controls vary across space and with scale.

6.6.0 References

Gosz, J. R. 1992. Gradient analysis of ecological change in time and space - Implications for forest management. *Ecological Applications* 2: 248-261.

Holtmeier, F. K. 2003. *Mountain Timberlines: Ecology, Patchiness, and Dynamics*. Springer, Berlin.

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

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

Little, J. E. L. 1971. *Conifers and Important Hardwoods*. US Department of Agriculture, Washington, DC.

Malanson, G. P., D. R. Butler, D. B. Fagre, S. J. Walsh, D. F. Tomback, L. D. Daniels, L. M. Resler, W. K. Smith, D. J. Weiss, D. L. Peterson, A. G. Bunn, C. A. Hiemstra, D. Liptzin, P. S. Bourgeron, Z. Shen, and C. I. Millar. 2007. Alpine treeline of Western North America: Linking organism-to-landscape dynamics. *Physical Geography* 28: 378-396.

Seastedt, T. R., W. D. Bowman, T. N. Caine, D. McKnight, A. Townsend, and M. W. Williams. 2004. The landscape continuum: a model for high-elevation ecosystems. *BioScience* 54: 111-121.

Strayer, D. L., M. E. Power, W. F. Fagan, S. T. A. Pickett, and J. Belnap. 2003. A classification of ecological boundaries. *Bioscience* 53: 723-729.