

THE EFFECTS OF FOSSORIAL MAMMALS ON ALPINE TREELINE
DYNAMICS IN THE AMERICAN WEST

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THE EFFECTS OF FOSSORIAL MAMMALS ON ALPINE TREELINE
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TABLE OF CONTENTS

ACKNOWLEDGEMENTS	v
LIST OF TABLES	xi
LIST OF FIGURES	xiii
ABSTRACT.....	xvi
CHAPTER	
1. INTRODUCTION.....	1
<i>Objectives and Hypotheses</i>	3
<i>Significance</i>	5
2. THEORETICAL FRAMEWORK	7
<i>Ecotones and Alpine Treeline</i>	7
<i>Ecological Niche</i>	9
<i>Treeline Theories of Formation and Control</i>	11
<i>Anthropogenic Treeline</i>	11
<i>Climatic Treeline</i>	14
<u>Temperature and Solar Radiation</u>	16
<u>Precipitation/Snow and Wind</u>	18
<i>Edaphic/Orographic Treeline</i>	21
<u>Soil Characteristics and Geology</u>	22
<u>Orographic Geomorphic Impacts</u>	24
<i>Zoogeomorphology and Ecosystem Engineering</i>	25
<i>Gophers</i>	29
<i>Marmots</i>	35
3. STUDY SITES GEOGRAPHY	41
<i>Glacier National Park</i>	41
<i>Climate</i>	42
<i>Vegetation</i>	43

	<i>Geology, Geomorphology, and Soils</i>	43
	<i>Study Sites</i>	45
	<i>Olympic National Park</i>	50
	<i>Climate</i>	51
	<i>Vegetation</i>	52
	<i>Geology, Geomorphology, and Soils</i>	53
	<i>Study Sites</i>	54
	<i>Similarities and Differences Between Study Sites and Parks</i>	60
4.	METHODS	67
	<i>Field Sampling</i>	67
	<i>Laboratory Analysis</i>	71
	<i>Statistical Analysis</i>	78
5.	RESULTS	82
	<i>Field Sampling</i>	82
	<i>Sub-local Scale</i>	82
	<i>Local Scale</i>	98
	<i>Landscape Scale</i>	118
	<i>Regional Scale</i>	120
	<i>Laboratory Analysis</i>	126
	<i>Germination Experiment</i>	129
6.	DISCUSSION AND CONCLUSIONS	134
	<i>Hypothesis 1- The Sub-local Scale</i>	134
	<i>Hypothesis 2 - The Local Scale</i>	138
	<i>Glacier National Park</i>	139
	<i>Olympic National Park</i>	140
	<i>Hypothesis 3 - The Landscape Scale</i>	142
	<i>Glacier National Park</i>	142
	<i>Olympic National Park</i>	143
	<i>Hypothesis 4 - The Regional Scale</i>	145
	<i>Hypothesis 5 - Chemical Soil Characteristics</i>	146
	<i>Hypothesis 6 - Seed Germination</i>	147

REFERENCES160

LIST OF TABLES

Table	Page
1. Elevational ranges, aspects, parent material, dominant treeline species, and climatic variables of study sites in both Glacier National Park, Montana and Olympic National Park, Washington	62
2. The purpose of each study method	71
3. Data for undisturbed sites within Preston Park, Glacier National Park, Montana.	84
4. Data for gopher-disturbed sites within Preston Park, Glacier National Park, Montana	86
5. Data for undisturbed sites at Divide Mountain, Glacier National Park, Montana.	92
6. Data for gopher-disturbed sites at Divide Mountain, Glacier National Park, Montana	94
7. Data comparing undisturbed soils to gopher-disturbed sites within Preston Park, Glacier National Park, Montana	100
8. Data comparing undisturbed soils to gopher-disturbed sites at Divide Mountain, Glacier National Park, Montana	101
9. Correlation data between undisturbed soil characteristics as well as gopher-disturbed soil characteristics within Preston Park, Glacier National Park, Montana	104
10. Correlation data between undisturbed soil characteristics as well as gopher-disturbed soil characteristics at Divide Mountain, Glacier National Park, Montana	105
11. Data comparing undisturbed soils to marmot-disturbed sites at Hurricane Ridge, Olympic National Park, Washington	107

12. Data comparing undisturbed soils to marmot-disturbed sites at Blue Mountain, Olympic National Park, Washington	108
13. Data comparing undisturbed soils to gopher-disturbed sites at Obstruction Point, Olympic National Park, Washington	109
14. Correlation data between undisturbed soil characteristics as well as marmot-disturbed soil characteristics at Hurricane Ridge, Olympic National Park, Washington	115
15. Correlation data between undisturbed soil characteristics as well as marmot-disturbed soil characteristics at Blue Mountain, Olympic National Park, Washington	116
16. Correlation data between undisturbed soil characteristics as well as marmot-disturbed soil characteristics at Obstruction Point, Olympic National Park, Washington	117
17. Data comparing undisturbed soils in Glacier National Park, Montana, to undisturbed soils in Olympic National Park, Washington	122
18. Data comparing fossorial mammal-disturbed soils in Glacier National Park, Montana, to fossorial mammal-disturbed soils in Olympic National Park, Washington	123
19. Results from laboratory soil analysis	128
20. Local scale germination results in Glacier National Park, Montana	131
21. Local scale germination results in Olympic National Park, Washington.	131
22. Landscape scale germination results in Glacier and Olympic National Parks	132
23. Control soil germination results for soil compaction observed in Glacier and Olympic National Parks.....	132
24. Regional scale results for seed germination in undisturbed and disturbed soils..	133

LIST OF FIGURES

Figure	Page
1. Anthropogenic treeline in the Sangre de Cristo Mountains of southern Colorado	13
2. Climatic treeline in the San Juan Mountains of southwestern Colorado	15
3. Edaphic/Geomorphic treeline surrounding Swiftcurrent Lake in Glacier National Park, Montana	22
4. Pocket gopher eskers at Divide Peak, Glacier National Park, Montana	35
5. Active Olympic marmot burrow in Olympic National Park, Washington	37
6. Olympic marmot burrow in Olympic National Park, Washington	38
7. Olympic marmot burrow.....	39
8. Study sites in Glacier National Park, Montana.....	46
9. Divide Peak study site, Glacier National Park, Montana.....	47
10. Preston Park, Glacier National Park, Montana	48
11. Typical gopher-disturbed meadow in Preston Park, Glacier National Park, Montana	49
12. Detailed photograph of gopher disturbance in a meadow in Preston Park, Glacier National Park, Montana	50
13. Study sites in Olympic National Park, Washington.....	55
14. Blue Mountain study site, Olympic National Park, Washington.....	57
15. Hurricane Hill study area, Olympic National Park, Washington	58

16. Obstruction Peak study site, Olympic National Park, Washington	59
17. Subalpine meadow undergoing conifer invasion near Obstruction Point in Olympic National Park, Washington	60
18. Northern pocket gopher (<i>Thomomys talpoides</i>).....	63
19. Olympic marmot (<i>Marmota olympus</i>) in Olympic National Park, Washington....	65
20. Stuewe and Sons' 'cone-tainer'	73
21. All cone-tainers were placed in holding trays and three runs of five replications were performed	75
22. Temperature data collected with a portable weather station at the site of cone- tainer experimental growth	76
23. Average daily solar radiation for the month of July	77
24. Average daily solar radiation for the month of September.....	78
25. Soil compaction and subsurface temperature data from six sample sites within Preston Park, Glacier National Park, Montana	89
26. Surface temperature and soil moisture data from six sample sites within Preston Park, Glacier National Park, Montana	90
27. Soil compaction and subsurface temperature data from four sample sites at Divide Mountain, Glacier National Park, Montana	96
28. Surface temperature and soil moisture data from four sample sites at Divide Mountain, Glacier National Park, Montana	97
29. Results of soil compaction and subsurface soil temperature data at Preston Park and Divide Mountain, Glacier National Park, Montana	102
30. Results of soil surface temperature and soil moisture data at Preston Park and Divide Mountain, Glacier National Park, Montana	103
31. Juvenile subalpine fir tree growing on an abandoned marmot burrow.....	110

32. Results of soil compaction and subsurface soil temperature data at Hurricane Ridge, Blue Mountain, and Obstruction Point, Olympic National Park, Washington	112
33. Results of soil surface temperature and soil moisture data at Hurricane Ridge, Blue Mountain, and Obstruction Point, Olympic National Park, Washington	113
34. Soil compaction and subsurface soil temperature data at Glacier National Park, Montana, and Olympic National Park, Washington	124
35. Soil surface temperature and soil moisture data at Glacier National Park, Montana, and Olympic National Park, Washington	125
36. A gopher esker in Preston Park, Glacier National Park, Montana.....	138

ABSTRACT

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Alpine treelines are often used to monitor climate change. However, caution should be exercised when these ecotone proxies are used to infer climate change.

Although climate has been shown to have a considerable influence on treeline location, many fine-scale processes are also accountable for treeline dynamics. The geomorphic effects of burrowing mammals may provide conifer seedlings with refuge in previously inhospitable treeline environments and may result in treeline dynamics that are not directly associated with climate change. In Olympic National Park, Olympic marmot

(*Marmota olympus*) populations have been declining (Griffin et al. 2008) and abandoned burrows may provide ideal sites for conifer establishment. Similarly, in Glacier National Park, pocket gophers (*Thomomys talpoides*) have disturbed large areas of alpine meadows at treeline, which may facilitate establishment. Substrate altered by gopher and marmot activity, when compared to adjacent, undisturbed areas, may provide ideal conditions for conifer seedling germination, emergence, and ultimate establishment. Gopher and marmot activity reduced soil compaction and such soils were typically drier than adjacent, undisturbed soils. Soils disturbed by gophers in GNP were cooler than undisturbed soils, whereas marmot-disturbed soils were warmer. Seed germination was higher on marmot-disturbed soils than on gopher-disturbed soils. Despite these experimental findings, no statistical difference existed in seed germination within control soils compacted to gopher and marmot rates observed in the field. It is likely, therefore, that although soil compaction appears to influence soil moisture and soil temperature, it may not be the ultimate driving force determining seed germination in mammal-disturbed soils. Additional research is needed to individually evaluate additional variables that may influence seed germination and survival in an alpine environment.

Keywords: alpine treeline, mountains, ecotones, biogeomorphology, zoogeomorphology, ecosystem engineering, Olympic National Park, Glacier National Park

CHAPTER 1

INTRODUCTION

Alpine and subalpine meadows, well renowned for their biodiversity and aesthetic appeal, have exhibited substantial change throughout the American West during the past century. Arguably, the most noticeable change has been that of conifer invasion into alpine and subalpine meadows. The principal driver of conifer invasion into meadows has been attributed to climate change and climate variability (Franklin et al. 1971; Butler 1986a; Taylor 1995; Butler et al. 2003; Camarero and Gutiérrez 2004). Cessation of intensive grazing practices in alpine and subalpine areas (Hansen et al. 1995; Grace et al. 2002), along with fire suppression during the 20th century (Arno and Gruell, 1983; Arno and Gruell, 1986; Magee and Antos 1992), has also been shown to facilitate conifer invasion into previously uninhabited meadows and alpine environments. Despite strong evidence of macro-scale controls on alpine treeline dynamics, such as those mentioned above, many micro-scale features act as nurse objects (Pérez 2002; Flores and Jurado 2003; Resler et al. 2005; Resler 2006) and have been shown to influence local pattern and process at alpine treeline. Compared to the undisturbed surrounding matrix, micro-scale sites disturbed by native animal activity in mountainous regions have displayed altered soil compaction characteristics (Butler and Butler 2009) and have exhibited altered vegetative structures (Sherrod and Seastedt 2001). Several studies have examined vegetative alterations associated with marmot (*Marmota*) disturbance in the United States

(del Moral 1984; Barash 1989; Plaster 2003), as well as pika (*Ochotona*) in Mongolia, Tibet, and the Himalaya (Bagchi et al. 2006; Wesche et al. 2007; Xinghu et al. 2007). Zokor (*Myospalax fontanierii*) mounds in Asia have also been shown to exhibit altered organic carbon in soils of animal disturbance and therefore, increased plant species diversity near abandoned burrows (Wang et al. 2008). Despite substantial research on micro-scale features, which create habitable sites for establishing vegetation, and the obvious impact of burrowing mammal activity on vegetative communities, no known research has attempted to apply these principles to conifer seedling germination and emergence at alpine treeline.

Glacier and Olympic National Parks provide ideal locations to assess climatic, orographic, and edaphic treeline dynamics (Whitesides and Butler 2011). Glacier National Park, Montana, (GNP) has high populations of Northern pocket gophers (*Thomomys talpoides*) in treeline environments and provides an opportunity to assess fossorial mammal/treeline dynamics in areas of stable mammal populations. The ubiquitous distribution throughout the park has created many sites that are continually disturbed by gophers. These disturbed areas may potentially result in lower conifer establishment rates caused by animal disturbance but it is more likely, however, that continual disturbance may enhance soil quality and increase seed germination. In Olympic National Park, Washington, (ONP) Olympic marmot (*Marmota olympus*) populations have declined (Griffin et al. 2008; Griffin et al. 2009). Griffin et al. (2008) identified that many historical colonies of Olympic marmots have disappeared and previously inhabited meadows and alpine environments are free of active marmots and now contain many abandoned burrows. Unlike the continual disturbance created by

pocket gophers in GNP, abandoned marmot burrows are free of continual marmot disturbance and may be more susceptible to colonization by conifer seedlings. Secondary to vegetation dynamics, establishment of conifers in gopher- and marmot-disturbed sites may have ramifications on fossorial mammal populations. Seedling establishment may produce a positive feedback by which animal disturbance may result in higher than average conifer establishment in alpine and subalpine meadows. Additional conifers may decrease suitable gopher and marmot habitat and be detrimental to animal populations at alpine treeline.

Objectives and Hypotheses

The objectives of this proposed research are:

1. Assess the importance of burrowing mammal activity on conifer seed germination in alpine treeline environments.
2. Through fieldwork and statistical analysis, determine the soil characteristics (both physical and chemical) associated with gopher and marmot disturbance as well as undisturbed soils across the alpine treeline ecotone in Glacier and Olympic National Parks.
3. Controlling for climatic variables and other exogenous disturbances, determine if successful conifer germination is more prevalent on mammal-disturbed soils compared to undisturbed soils.
4. Determine if disturbance from two different fossorial mammals in two different national parks, pocket gophers in GNP and marmots in ONP, have significantly

different impacts on soil characteristics and subsequently, conifer germination dynamics.

In order to meet the objectives mentioned above, several hypotheses will be tested to evaluate the impact of fossorial mammals at treeline. Hypotheses will be evaluated at four different scales, sub-local, local, landscape, and regional. The sub-local scale will evaluate differences in undisturbed soils within study areas, as well as differences between disturbed soils within the same study areas. The local scale will evaluate the differences between mammal-disturbed and undisturbed soil characteristics at each area and assess possible connections that exist between mammal disturbance and seed germination. At the sub-local scale, one hypothesis will be evaluated:

H₀1: Physical soil characteristics (soil compaction, surface and subsurface temperatures, soil texture, and soil moisture) are the same for all undisturbed sites within a study area and all mammal-disturbed sites within a study area are equal.

Several hypotheses exist at the local scale and the null hypotheses include:

H₀2: Physical soil characteristics (soil compaction, surface and subsurface temperatures, soil texture, and soil moisture) are the same between locations of mammal disturbance and undisturbed areas within a study area.

At the landscape scale (approximately 20-25 linear km between locations), differences between study areas will be assessed. The null hypothesis is:

H₀3: There is no difference in physical soil characteristic between Preston Park, GNP, and Divide Mountain, GNP. Furthermore, no difference is expected between Hurricane Ridge, ONP, Blue Mountain, ONP, and Obstruction Point, ONP.

At the regional scale (approximately 720 linear km between locations), undisturbed and mammal-disturbed soils in GNP will be compared to undisturbed and mammal-disturbed soils in ONP. The null hypothesis states:

H₀4: There is no difference in physical or chemical soil characteristics of undisturbed or mammal-disturbed soils in GNP and ONP.

In addition to the hypotheses examining physical soil characteristics at different scales, chemical soil characteristics will also be addressed with a null hypothesis that states:

H₀5: Chemical soil characteristics (pH, salinity, P, K, and organic matter) are the same between locations of mammal-disturbed and undisturbed areas within a study area.

In addition to both physical and chemical soil characteristics, subalpine fir germination will be examined in soils collected from both national parks. The null hypothesis is:

H₀6: Standardizing temperature and precipitation, subalpine fir germination will be the same in both undisturbed and mammal-disturbed soils at all scales and independent of soil compaction.

Significance

The nature of this project is mostly theoretical and combines aspects from both the biological and earth science disciplines in an attempt to analyze treeline dynamics in a more holistic approach. Past biological research has examined vegetation at alpine treeline and documented both physiological and morphological characteristics of treeline species. Ecologists have found that vegetation near animal burrows can be significantly

different from vegetation not associated with animal disturbance. Climatologists and others have attempted to use treeline fluctuations as proxies for climate change and subsequently, historical studies on alpine treeline ecotones have been primarily focused on climate as a control of treeline. More recently, however, ecologists and geomorphologists have expanded research of treeline controls to include nurse objects, feedbacks, and geomorphology. Despite these advances by several disciplines, little research has attempted to identify circumstances under which burrowing animals affect treeline dynamics and this study attempts to fill an important theoretical gap.

The application of this study has broader ramifications. As mentioned previously, alpine treeline has long been utilized as a proxy for climate change, and better understanding of treeline dynamics that are not climatically induced may reveal that some treeline environments are constrained by non-climatic factors and may be less than ideal proxies for climate change. Furthermore, treeline processes that affect alpine and subalpine meadow environments are of concern to federal land managers. The unique flora of these environments, replete with summer flowers and the vistas above treeline, have become iconic of western National Parks and annual visitation and revenue may be affected if these resources are disturbed, reduced, or eliminated.

CHAPTER 2

THEORETICAL FRAMEWORK

Ecotones and Alpine Treeline

According to the Scientific Committee on Problems on the Environment (SCOPE), an ecotone is “a zone of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales and by the strength of the interactions between adjacent ecological systems” (Holland 1988, p. 48). This definition suggests that natural ecosystems are not static phenomena but are dynamic and, therefore, ecosystem boundaries are in a state of constant flux (Wiens et al. 1985; Gosz 1991). Furthermore, ecotones consist of a mixture of floral and faunal characteristics and processes found in both neighboring ecosystems (Allen and Starr 1982) and may provide essential habitat, or act as corridors, for many species (Beier and Noss 1998; Fagan et al. 1999; Damschen et al. 2006). Ecotones have also been shown to be sensitive to climatic conditions and are actively used as proxies for climate change (di Castri et al. 1988; Noble 1993; Allen and Breshears 1998; Butler et al. 2009). Unlike climatic proxies such as packrat middens or ice cores that are spatially confined to arid desert environments or cryospheric regions, ecotones exist in all biomes at a variety of spatial scales. The ubiquitous nature of ecotones, therefore, provides a more suitable medium to monitor environmental change. Furthermore, packrat middens and ice cores

provide a historical record of climate over long temporal periods but are typically poor proxies of change over short temporal scales. Ecotones, on the other hand, provide an important medium by which environmental change may be monitored over greater spatial scales and shorter temporal periods. The alpine treeline ecotone has become an icon for environmental change (Kullman 2001).

Alpine treeline is a distinct threshold in many mountain environments that demarcates the closed canopy forest from the alpine tundra. Above the treeline, it is disadvantageous, or unaffordable, for large, single-stemmed trees to establish and persist (Körner 1998). The transitional nature of the alpine treeline ecotone has generated some debate as to how treeline should be distinguished and delineated. Hustich (1979) argued that ecological concepts were lacking consistent terminology and alpine treeline is a prime example of differences in terminology. Timberline, a somewhat dated yet common term, has been defined as “the upper limit of tall, erect timber-sized trees” (Wardle 1965, p. 113). Timberline has also been used more ambiguously as “the limit of forest either high up on mountainsides, in frigid polar regions, or in adjacent grasslands” (Arno and Hammerly 1984, p. 11). Wardle (1974) also defined timberline as the broad ecotone between two different habitats. Although early definitions cited timberline as an ecotone, the dynamic nature and processes of ecotones were not fully understood nor explained. More specific categorization of the timberline resulted in “tree limit” (Wardle 1974) or “tree line” (Arno and Hammerly 1984), which were identified as the limit of erect individual trees. Tree limit/tree line is different from the “forest limit” (Wardle 1974), which is defined as areas where trees grow sufficiently close to create a closed canopy. Upslope from the closed canopy and the treeline, stunted and deformed trees have been

termed “krummholz” and typically mark the altitudinal limit of conifer species (Wardle 1974; Holtmeier 1981; Arno and Hammerly 1984). The multiple altitudinal zones of the alpine treeline ecotone have provided important distinction between treeline processes and have provided theoretical frameworks for a variety of research. Today, the alpine treeline ecotone is recognized as more than the mere sum of its parts but is assessed more fully as a transitional area from closed canopy forest to alpine tundra, which is not stable but is in a state of flux dominated by many processes. Most recently, the alpine treeline ecotone has been defined as the area extending from closed canopy forest, upslope to the tundra (Fagre 2009). The current alpine treeline ecotone includes what has traditionally been classified as both “tree limit” and krummholz. The processes that control and shape the alpine treeline ecotone have intrigued scientists for years, and alpine treeline has become an important indicator of climate change despite some skepticism that the lag-time between climate change and the result on the land surface make treelines a less-than-ideal proxy for change (Kupfer and Cairns 1996). Alpine treeline patterns and processes, whether they are associated with climate or some other factor, are ultimately based on the theory of ecological niche.

Ecological Niche

Initially, ecological niche theory developed as a method to explain the geographic distribution of fauna but application quickly expanded to address floristic distributions. In the early 20th century, Joseph Grinnell (1904, 1917, 1924) theorized that species distribution was determined by environmental or ecological requirements. He postulated that abiotic factors such as substrate and climate were instrumental in determining the

distributional limits of a species. Although Grinnell's ideas were well founded and successfully described the distribution of many species, Charles Southerland Elton contended that species distribution was not solely based on abiotic factors but also included interaction and competition with other organisms in the ecosystem. Elton (1927) based his theory on resource requirements and partitioning, and determined that an organism could not survive in an environment where it was outcompeted for resources.

In 1957, ecological niche theory was re-conceptualized to highlight the differences between Grinnell and Elton's theories. Hutchinson (1957) stated that Grinnell's theory of necessary abiotic requirements for a species to survive was the 'fundamental niche', or the location where a species could exist with no competition. Elton's theory was termed the 'realized niche', or habitable environment where the 'fundamental niche' conditions were met as well as positive and negative interactions between neighboring organisms (Hutchinson 1957).

Further advancement in niche thinking highlighted the difference between the realized niche of juvenile to adult plants to the niche required for germination and the initial establishment of a species. Grubb (1977, p. 119) defined the regeneration niche as, "the requirements for a high chance of success in the replacement of one mature individual by a new mature individual of the next generation". Although Grubb's definition of the regeneration niche highlights the replacement of species, this concept is also applicable to the generation of species following disturbance or in areas where the species has not previously existed. Seedling establishment in canopy gaps created by treefall, for example, demonstrate that disturbance and a host of microsite controls

influence the regeneration niche of a variety of species (Veblen 1986; Gray and Spies 1997). Following fire disturbance, a finite period exists for ideal white spruce establishment. Beyond three or four years post-fire, the conditions of the regeneration niche for white spruce deteriorate and competing species dominate (Purdy et al. 2002). In previously unoccupied locations successful establishment of subalpine fir in Wyoming, USA, has been attributed to the positive effect associated with neighboring whitebark pine, which enhance the regeneration niche of subalpine fir (Maher and Germino 2006). Although both belowground (soil moisture, soil compaction, etc.) and aboveground (canopy height, light intensity, etc.) requirements may be necessary to satisfy an organism's regeneration niche (Silvertown 2004), this research focuses on the belowground components. As will be demonstrated below, much early treeline research focused on fundamental niche aspects associated with climate. More recently, however, treeline processes have expanded to evaluate the realized and regeneration niches where more complex abiotic factors and disturbances, coupled with competition and interaction between and among species, have created more complex treeline dynamics.

Treeline Theories of Formation and Control

Anthropogenic Treeline

Holtmeier and Broll (2005) classified alpine treeline into three distinct types depending upon the process by which the treeline developed. Their three-treeline classifications are anthropogenic, climatic, and orographic/edaphic treeline. In Europe, anthropogenic treelines are common because of long-term settlement in mountain environments and extensive human-environment modification (Motta et al. 2006). In the

western United States, anthropogenic treelines are not as evident as their European counterparts. Although population expansion during the 19th and 20th centuries drastically modified mountain environments and treeline dynamics, the direct changes generally occurred at lower treeline environments adjacent to settled areas. In some alpine environments, however, forestry and lumbering occurred near treeline and resulted in dramatic anthropogenic treelines (Figure 1). Direct human impacts on alpine treeline are less frequent than indirect effects associated with fire suppression and grazing which are generally less conspicuous and not immediately evident. Over time, extensive fire suppression throughout the West increased forest cover and altered forest vegetation dynamics (Taylor 2000). Livestock grazing has had various effects on treeline. Light to moderate livestock grazing at high elevations in the West has benefited juvenile trees, whereas, heavy grazing has resulted in high trampling mortality and has been detrimental (Dunwiddie 1977; Butler 1986a; Vale 1987). In some instances in European mountain ranges, the cessation of anthropogenic activity at treeline has allowed some woody species to reestablish at elevations consistent with undisturbed treelines (Holtmeier 1994; French et al. 1997). In other instances, however, the anthropogenic affect on alpine treeline landscapes has drastically altered local site conditions (e.g. amount of insolation, wind velocity and direction, duration of snowcover, soil temperatures, etc.) such that trees are unable to reestablish in human-impacted areas and treeline control transitioned from anthropogenic factors to a treeline that is controlled by climatic processes (Holtmeier and Broll 2005). In Finland, for example, tree establishment in areas once dominated by anthropogenic processes have experienced only marginal reestablishment because of climatic micro-site factors that impede future establishment despite globally

warming temperatures (Holtmeier et al. 2003). Although anthropogenic treeline is not the scope of this study, it is important to note that treeline in National Parks, which are generally protected from direct anthropogenic disturbance, are not exempt from the effects of fire suppression or human-induced climate change. Furthermore, grazing was permitted in some parks prior to their designation as National Parks. Anthropogenic effects on treeline are mitigated in National Parks but nowhere are treelines completely free of human disturbance.



Figure 1. Anthropogenic treeline in the Sangre de Cristo Mountains of southern Colorado. Photo by David R. Butler.

Climatic Treeline

All plant communities are spatially defined by environmental gradients that control species density and distribution (Dale 1999). In mountain environments, latitude, elevation, and topography have been suggested as the most influential gradients that control climate and subsequently, plant communities (Billings 1994). Many alpine treeline environments are controlled by climatic variables (Figure 2). Latitude determines insolation and is, thus, the primary driver of north-south trending temperature gradients and suitable climate for species distribution at a continental and hemispherical scale. Elevation has potential to modify latitudinally induced climate at the landscape scale of individual mountain ranges. Hanawalt and Whittaker (1977) found that elevation was a major component in the location of wild oats (*Avena fatua*) in the San Jacinto Mountains of California. Soil nutrients were associated with climatic conditions across an elevational gradient with increased nutrients at low, warm elevations. Like wild oats, conifer forests in mountainous regions of the western United States have also been influenced by climatic conditions associated with elevation. Arno and Hammerly (1984) found that lower elevations in the mountainous western United States often received insufficient annual precipitation to support conifer forests. Conifers located near the limit of the moisture gradient could not survive and a forest/grassland ecotone developed. At finer spatial scales, the environmental gradients of latitude and elevation are often modified or superseded by topography. It has long been recognized that aspect is capable of supporting distinctly different vegetative communities over short distances (Blumer 1910). Differences in insolation, temperature, moisture, and plant communities and

densities may exist over relatively short distances where topography modifies the local climate (Cantlon 1953). North-facing slopes in Chile receive more insolation and support vegetation that is capable of withstanding more xeric conditions than vegetation on east, west, or south-facing slopes (Armesto and Martínez 1978). At alpine treeline, latitude, elevation, and topography have substantial impacts on the climatic variables of temperature, solar radiation, precipitation, and wind.

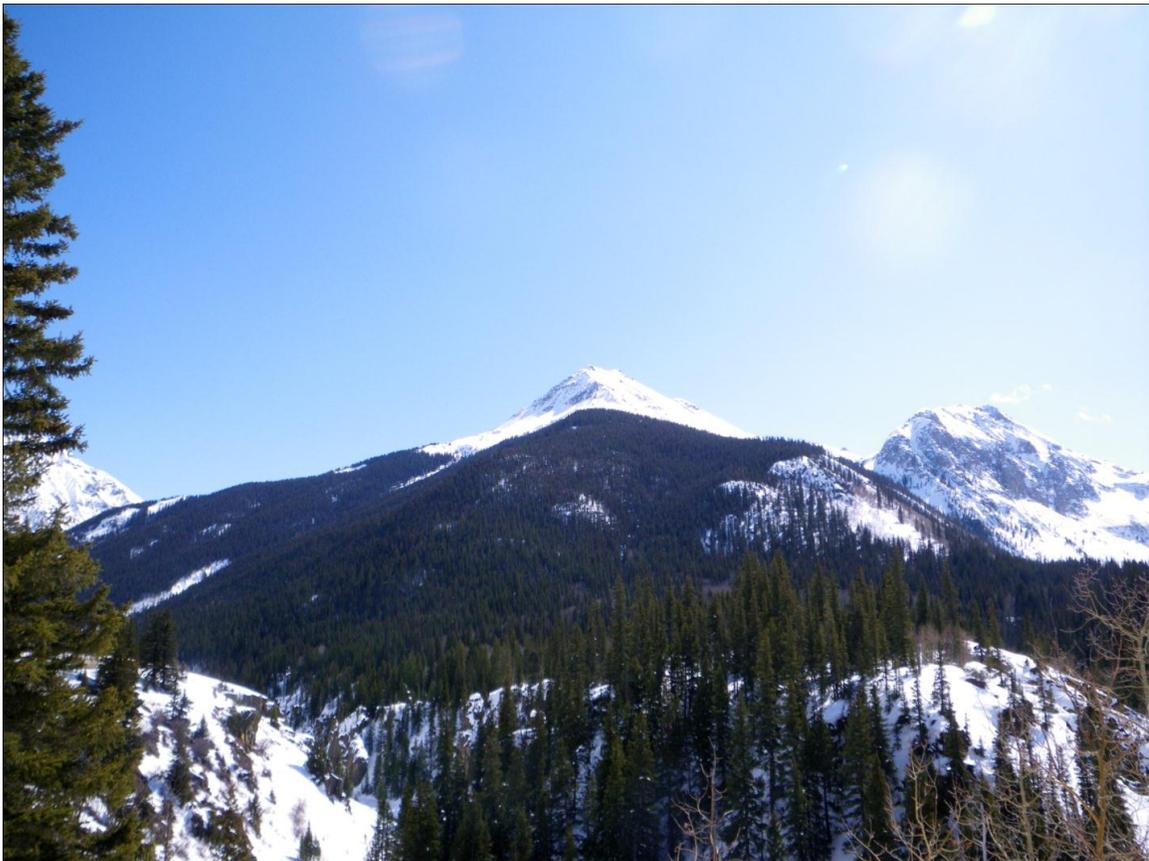


Figure 2. Climatic treeline in the San Juan Mountains of southwestern Colorado. Notice the consistent elevation between closed canopy forest and snow covered tundra across the mountain.

Temperature and Solar Radiation

Latitude, elevation, and topography have substantial effects on both temperature and solar radiation in mountain environments. At a continental scale, Wardle (1974) suggested that fluctuations in treeline elevation were controlled by annual temperature. Low annual temperatures associated with high elevations often result in a short growing season. However, Wardle (1974) noted high correlation between treeline elevation and warm summer temperatures, whereas, cold winter temperatures had little effect on treeline. In Yellowstone National Park, modeled climate scenarios suggested that alpine treeline is likely to move upslope under warmer climatic conditions (Romme and Turner 1991) and fieldwork identified that subalpine meadows have experienced lodgepole pine invasion associated with warmer and wetter growing conditions since the end of the Little Ice Age (Jakubos and Romme 1993). Similar findings exist in the Rocky Mountains of Colorado (Hessl and Baker 1997). At a global scale, it has been hypothesized that a minimum temperature exists below which new cell production is inhibited in treeline species (Körner 1998). In the Snowy Mountains of Wyoming, Germino et al. (2002) found that subalpine fir and Engelmann spruce seedlings had highest survival rates during years when the mean difference in daily maximum and minimum temperatures was smallest and experienced lower survival rates when above-average temperatures coincided with reduced precipitation. Temperature is undoubtedly a primary control of alpine treeline throughout the world and continues to be a topic of much research in the mountains of western North America (Butler et al. 2004; Case and Peterson 2005; Nakawatase and Peterson 2006; Schrag et al. 2008).

In addition to temperature, solar radiation also impacts photosynthetic carbon gain and may be a controlling factor at treeline. Schulze et al. (1967) calculated that more than 117 hours of peak summer photosynthesis would be required to remedy the negative CO₂ balance found in bristlecone pines in the White Mountains of California. One-hundred and seventeen hours of peak photosynthesis is equivalent to half of the growing season at this location. The authors concluded that photosynthesis may be a limiting factor at treeline. Seedlings and juvenile trees appear to be especially susceptible to variations in photosynthetic carbon gain. Seedlings on cooler, north-facing slopes have been shown to have lower CO₂ uptake rates than seedlings at equivalent elevations on eastern aspects (Häsler 1982). In the mountains of Scotland, photosynthetic capabilities of juvenile Scots pine above treeline were compared with trees in a valley environment during the month of June. Pines above treeline had lower photosynthetic performance than valley trees. The authors cited lower temperatures at treeline as the cause of photoinhibition and stated that differences in photosynthetic capabilities between treeline and valley trees were nonexistent by late summer (James et al. 1994). In Wyoming, seedlings growing at treeline, as compared to seedlings below the ecotone in a more closed canopy environment, experienced reduced rates of photosynthesis because of low-temperature photoinhibition (Germino and Smith 1999, 2000). Nighttime temperatures below 2°C were responsible for delayed photosynthetic activity the following day (Johnson et al. 2004). These examples suggest CO₂ uptake may be a limiting factor of tree growth at treeline. Under speculation of a warming climate and increased CO₂ concentrations, it has been suggested that net primary productivity in conifers may increase and be capable of sequestering substantial amounts of anthropogenic CO₂

(DeLucia et al. 1999; Hättenschwiler et al. 2002). However, data from high elevation treeline sites in Mexico, the Alps, and Northern Sweden suggest that tree growth is not carbon-limited but is constrained by poor cell growth associated with low temperatures (Körner 2003). Despite these findings, it is more likely that photosynthetic carbon gain is a factor of treeline control at many local treeline sites. Simulated environmental variables revealed that temperature was indeed important in treeline carbon balance, but winter injury and tree physiognomy also influenced carbon balance (Cairns and Malanson 1998; Cairns 2005). Variations in microsite solar radiation have also been suggested as a controlling factor of photosynthetic carbon balance at treeline (Brodersen et al. 2006). Notwithstanding the importance of temperature and photosynthetic carbon gain at alpine treeline, it is clear that additional climatic factors contribute to these processes and influence treeline form and function.

Precipitation/Snow and Wind

Precipitation has been shown to have substantial impacts on alpine treeline dynamics. Precipitation in mountain landscapes is controlled greatly by local topography. Kruckeberg (2002, p. 87) even suggested that, “weather systems are products of the mountain systems they encounter.” This concept is well illustrated in the Olympic Mountains of western Washington. Rapid elevational change from sea level to the summit of Mount Olympus (2432 m) in a distance of approximately 50 km has created a dichotomous precipitation regime (NPS 2008). The western side of the mountain range is subject to orographic lift and receives more annual precipitation (3810-5080 mm) than any other location in the contiguous United States. Orographic lift has

created a substantial rain shadow on the eastern or leeward side of the range where precipitation averages 431.8 mm (Arno and Hammerly 1984). Although moisture tends to be more of a controlling factor at lower treeline than alpine treeline (Weltzin and McPherson 2000; League and Veblen 2006), scholars have noted that forest dynamics at and below alpine treeline are susceptible to moisture variability. Under drier than normal climate conditions, subalpine fir preferentially established in more mesic subalpine meadows (Woodward et al. 1995). Warmer and wetter climate scenarios suggested as an outcome of climate change may also facilitate subalpine fir growth at higher elevations (Ettl and Peterson 1995). In the Sierra Nevada, conifer seedlings were able to invade subalpine meadows during periods of increased minimum monthly temperatures and increased moisture (Millar et al. 2004) and a significant relationship was shown between monthly precipitation and tree growth (Graumlich 1991). Similarly, high mortality occurred in conifers in the Snowy Range of Wyoming during periods of low rainfall, increased temperatures, and clear skies (Germino et al. 2002).

In many alpine environments, snow remains on the landscape well into summer months. In these types of environments, too much or too little snow can be both beneficial and detrimental to treeline dynamics (Cox 1933). Substantial snowpack can partially or fully bury trees and insulate them from temperature extremes, radiation, and damaging winds (Billings and Bliss 1959; Daly 1984; Walsh et al. 1994; Camarero et al. 2000). In the Pyrenees Mountains, krummholz at treeline enhanced snow deposition and provided adequate soil moisture for seedling establishment in the spring (Camarero et al. 2000). Similar findings exist on the Beartooth Plateau of Wyoming where whitebark pine seedlings established in mesic areas of late-lying snow (Mellmann-Brown 2005).

Although snow provides many benefits to alpine trees, trees not buried fully by snow are susceptible to foliage desiccation from high winds and stem breakage that may effectively limit treeline elevation and stunt conifers to krummholz form (Baig and Tranquillini 1980; Hadley and Smith 1983, 1986, 1989). In Glacier National Park, Cairns (2001) found that windward segments of krummholz patches experienced more desiccation than leeward segments. During the 1998-1999 winter, nearly nine percent of sampled krummholz canopy was lost to desiccation (Cairns 2001). On Mount Washington, New Hampshire, however, wind was not found to be the universal cause of winter desiccation (Marchand and Chabot 1978). Furthermore, the effects of wind on treeline pattern and position are complicated further by the fact that wind was cited as the primary factor inhibiting upward migration of treeline along the Colorado Front Range (Daly and Shankman 1985) and has been thought to delay or preclude seedling establishment at treeline (Holtmeier and Broll 2010), whereas, in Glacier National Park, wind has been shown to have a positive feedback on treeline pattern and process (Alftine and Malanson 2004). In subalpine ribbon forest environments, late-lying snow in snow glades between ribbon forests has been suggested as a mechanism by which ribbon forests are maintained (Billings 1969). The wet meadow environments created by late-lying snow may inhibit conifer infilling of subalpine meadows and one study in the mountains of Norway showed a significant correlation between treeline growth rate and snow depth (Dalen and Hofgaard 2005) which most likely is the result of the aforementioned benefits and detriments of snowcover on alpine treeline vegetation.

Edaphic/Orographic Treeline

The final treeline classification identified by Holtmeier and Broll (2005) is that of edaphic/orographic treeline. In many treeline environments, the actual treeline elevation is restricted despite climatic conditions that would otherwise allow treeline to extend to higher elevations (Figure 3). In these locations, edaphic characteristics and geomorphic processes common to mountain environments (e.g. active talus cones, avalanche chutes, etc.) hinder the advancement or establishment of trees and suppress alpine treeline (Butler and Walsh 1994; Resler 2006; Butler et al. 2007).



Figure 3. Edaphic/Geomorphic treeline surrounding Swiftcurrent Lake in Glacier National Park, Montana. Notice the elevation of climatic treeline on the right side of the photo (arrow) compared to the depressed elevation of treeline on the left side of the photo. Active talus impedes the upward migration of treeline despite climatic conditions that would normally allow treeline to exist at higher elevations.

Soil Characteristics and Geology

Soil characteristics are a product of many of the aforementioned climatic controls on treeline. The redistribution of snow by wind has been shown to modify soil characteristics (Hiemstra et al. 2006) and eolian sediments are common in alpine soils of Colorado (Muhs and Benedict 2006). Subsequently, the association between vegetation and underlying soil in mountain environments of the western United States is a well-documented process of treeline control. In the White Mountains of California, Mooney

et al. (1962) found that conifers between 2895 and 4115 meters above sea level grew at higher elevations on dolomitic substrate than on granitic or sandstone substrates. In Glacier National Park, Bamberg and Major (1968) noted the relationship between calcareous parent material and vegetation near treeline and soil derived from parent material was cited as exerting the greatest control on plant community development on the mountain slopes of Crater Lake National Park, Oregon (Jackson and Faller 1973). In addition to parent material, Spomer and Salisbury (1968) proposed that treeline was dependent upon soil temperature and speculated that cold soil temperatures inhibited root growth and function. The interaction between soils and vegetation is not unilateral and alpine treeline species have modified and enhanced local soil properties. Soil modifications in the Alps (e.g. plant macrofossils and charcoal) indicate that conifer species once existed at elevations higher than the present treeline (Tinner et al. 1996). Holtmeier and Broll (1992) stated that tree islands modify soil characteristics by collecting snow and eolian sediments, which alter soil moisture and texture. More recently, migrating tree islands have been shown to have an effect on soil nutrients which promote continued conifer establishment (Parker and Sanford 1999; Seastedt and Adams 2001) and create positive feedback at the local scale (Malanson 1997, 2001; Callaway 1998). Despite the clear impact soil characteristics have on treeline vegetation, not all soil characteristics affect vegetation. Malanson et al. (2002) found that effective soil depth did not appear to control directly vegetation patterns at treeline in Glacier National Park, Montana.

Although less studied than soil, underlying geology and exposed bedrock also exert control on treeline. At lower treeline, rocky outcrops and weathered glacial erratics

supported conifer trees in a moisture-limited, forest/grassland environment (Whitesides and Bekker 2011). In subalpine ribbon forest environments, well-drained, rocky ridges were dominated by conifers, whereas, lower elevation, inter-ridge locations were dominated by meadow species (Butler et al. 2003). The authors suggested that late-lying snow precluded conifers from adjacent meadows. Surficial geology, coupled with climate, has been cited as a primary control of treeline in GNP (Cairns and Waldron 2003) and similar findings suggest that subalpine fir trees are more likely to establish on topographic convexities where snow melt out occurs more rapidly and results in a longer growing season (Rochefort and Peterson 1996).

Orographic Geomorphic Impacts

Geomorphic impacts on treeline occur at several scales in mountain environments. Butler et al. (2009) identified coarse, medium, and fine-scale geomorphic processes present at treeline. At coarse-scales, snow avalanches and debris flows are capable of disturbing treeline dynamics. Snow avalanches have been shown to extend into the forest and destroy or damage existing trees. Snow avalanches commonly result in a depressed treeline that is maintained by short avalanche recurrence intervals (Patten and Knight 1994; Walsh et al. 1994; Butler and Malanson 1985, 1990, 1992; Butler 2001). During summer months, debris flows are also capable of extending into the ecotone and reducing the elevation of treeline (Butler and Walsh 1994). Steep, unconsolidated cinder slopes of Crater Lake National Park were incapable of supporting woody plants except in locations behind large lava boulders where the downward movement of rock debris was minimized (Jackson and Faller 1973). Medium-scale

geomorphic processes include turf-banked terraces from the Pleistocene, which appear to retard treeline advancement (Malanson et al. 2002), and eolian processes that have potential to erode and deposit sediment at treeline (Butler et al. 2009).

The importance of fine-scale processes on treeline dynamics has become evident in past decades and much research has attempted to identify the impact of individual fine-scale processes. Continuing with Butler et al.'s (2009) classification of geomorphic processes at alpine treeline, fine-scale processes include turf exfoliation, boulders, and frost heaving and churning. Butler et al. (2004) found that areas of exfoliated turf were more penetrable than non-exfoliated areas and suggested turf exfoliated sites as ideal microsites for conifer establishment. Boulders have been noted as important features associated with seedling establishment at treeline because of the modified microclimate adjacent to boulders that allowed for increased seedling establishment (Resler et al. 2005; Resler 2006). Not all fine-scale processes improve seedling establishment and survival. Continued frost action in solifluction treads and risers (Sawyer 2007) may inhibit seedling recruitment at treeline (Butler et al. 2009). Regardless of whether soils, geology, or geomorphology benefit or adversely affect treeline species, it is clear that edaphic and geomorphic processes in alpine environments exert substantial control over treeline function and pattern.

Zoogeomorphology and Ecosystem Engineering

Traditional geomorphology from the 19th and 20th centuries focused on established geomorphic principles such as weathering, volcanism, and fluvial, glacial and eolian processes but examined these processes in a world void of life (Butler 1995).

Many geomorphologists were trained in earth science disciplines and had a poor background in the biological sciences. In 1988, Heather Viles' seminal work, *Biogeomorphology*, addressed the relationship between geomorphology and biology, and biogeomorphology quickly evolved into a strong sub-discipline of geomorphology with particular emphasis on vegetative effects on geomorphology. In 1992, while examining the geomorphic effects of grizzly bears in Glacier National Park, Butler coined the term zoogeomorphology and highlighted the difference between plants and animals as geomorphic agents. Since that time, the biological sciences have had a more substantial role in geomorphology and scientists have examined animals as geomorphic agents.

It is important to note that the establishment of biogeomorphology and zoogeomorphology coincided with similar theories in the disciplines of biology and ecology. In 1994, Clive Jones and colleagues developed the paradigm of ecosystem engineering. This paradigm stated that flora and fauna were capable of modifying their local environment for their benefit. This paradigm differed from biogeomorphology and zoogeomorphology in that it did not focus on the relocation of materials by organisms and the landforms created by relocated material, but was interested in how plant and animal activity modified local environments (Jones et al. 1994). Extensive ecological research has examined the physical and chemical changes on substrate, modified climate, and positive and negative feedbacks between and among organisms and their environments (Jones and Shachak 1990; Jones et al. 1994; Callaway 1995; Jones et al. 1997; Wright et al. 2002).

Both biogeomorphology and ecosystem engineering have become important sub-disciplines of geomorphology and ecology, and both fields have become increasingly

complex. Recently, many proponents of ecosystem engineering have noted the importance of displaced sediment and the creation of new landforms and how these features impact plants and animals (Gutiérrez et al. 2006; DeVries 2012; Statzner 2012). Additionally, traditional biogeomorphologists have begun examining changes in local environments and how organisms modify their surroundings and the distinctive patterns these processes create (Alftine and Malanson 2004; Bekker 2005). The line between disciplinary boundaries has become increasingly obscure, as both scientists of biogeomorphology and ecosystem engineering have recognized the importance of one another's work.

Early studies of mammals as geomorphic agents focused on livestock. Localized soil disturbance associated with pig hoof marks noted an enhancement in *Plantago* seed reproduction of suggested the importance of soil surface disturbance for seedling establishment (Harper et al. 1965). Early research on cattle emphasized the negative effects of grazing cows in riparian zones (Kauffman et al. 1983). Kauffman and Krueger (1984) identified that grazing cattle removed vegetation, which resulted in increased erosion along riverbanks. Despite these findings, full quantitative analysis was not achieved until the prominent study by Trimble and Mendel (1995). The findings of Trimble and Mendel quantitatively demonstrated that heavy cattle grazing increased soil compaction, reduced moisture infiltration, and enhanced surface runoff and erosion. In riparian areas, the findings of Trimble and Mendel (1995) were consistent with those of Kauffman and Krueger (1984). In addition to erosion caused by soil compaction, direct erosional impacts of cattle grazing resulted in increased slope failure and increased erosion and sediment transport (Trimble 1994; Trimble and Mendel 1995). The impact

of domesticated animals as geomorphic agents has been well documented (Evans 1998) and continues to be studied in various environments (Butler 2006; Isselin-Nondedeu et al. 2006; Isselin-Nondedeu and Bédécarrats 2007).

The significant impact of domesticated animals on landscape shape and form is easily recognized. The impact of wild animals on the landscape however, is often difficult to recognize and even more difficult to quantify. The major exception is that of beaver (*Castor*). Beaver ponds are easily recognizable and have a definite effect on fluvial geomorphology. Subsequently, beaver have likely been the most studied animal as a geomorphic agent (Ffolliott et al. 1976; Butler and Malanson 1994; Butler 1995). Following beavers, much zoogeomorphic research has focused on burrowing mammals (Butler 1995).

For the various reasons cited above, ecotones are ideal locations to study zoogeomorphology. Alpine environments, and ecotones in particular, contain an abundance of wild animal species and disturbances are often more readily identifiable along ecotones than within the core of an ecosystem (Butler 1992; Hall et al. 1999; Hall and Lamont 2003). Butler (1992) found that grizzly bears in Glacier National Park were capable of removing more sediment than snow avalanches each year and Hall et al. (1999) found similar results for grizzly bear excavations in Canada. Doak and Loso (2003) emphasized the effects of grizzly bears on local vegetation in alpine regions, but focused on the reduction in species richness associated with bear disturbance rather than specific geomorphic effects. Much research has focused on the impressive erosional capabilities of grizzly bears, but many smaller mammals are also capable of causing erosion and altering vegetation dynamics. In long-term vegetation monitoring plots in

subalpine meadows at Logan Pass in GNP, Columbian ground squirrel (*Citellus columbianus*) excavations decreased vegetation cover over a 30-year period (Hartley 2000). Although many burrowing mammals are active in the alpine treeline ecotone (e.g. ground squirrels, mice, voles, pika, etc.), a complete review is beyond the scope of this analysis (readers are referred to Butler (1995) and Hall and Lamont (2003) and references therein as a starting point). Only gophers and marmots will be discussed in this manuscript.

Gophers

Northern pocket gophers (*Thomomys talpoides*) are rodents that are typically between 165-235 mm in length and weigh between 78-130 g (Streubel 2000). They have long claws that are well adapted to digging (Figure 18) and are primarily solitary animals whose distribution is widespread and whose population is not in jeopardy of collapse (Streubel 2000). Pocket gophers do not hibernate and remain active throughout the year. In Utah, a single pocket gopher dug more than 146.3 m of tunnel in a five-month period and excavated an estimated 481.7 kg of soil (Richens 1966). In California, pocket gophers were estimated to be capable of moving 17.9 metric tons per hectare per year (8 tons per acre per year; Grinnell 1923). Pocket gopher home ranges occupy approximately 125-170 m² (Streubel 2000) and have been estimated at densities of 11.1 per ha (Ellison 1946) and observed at densities of 81.5 per ha in Utah (Ellison and Aldous 1952).

Many studies of fossorial mammals have examined the impact of gopher mounds and eskers on soil conditions and local plant communities. In 1942, Larrison stated that

plant succession occurred on gopher mounds in the State of Washington and since that time, much research has examined the physical and chemical characteristics of gopher-disturbed soil. Much pocket gopher research has been conducted in subalpine meadows where gopher population densities are high and in alpine areas above treeline where population densities tend to be intermediate (Hansen and Bear 1964). In subalpine environments, gophers have been shown to preferentially occupy meadows with deep soils, whereas, alpine soils occupied by gophers are typically shallower than non-occupied alpine soils (Hansen and Beck 1968). The soil of gopher eskers and mounds often indicates the soil horizon from which the soil originated. In southwestern Colorado, gopher eskers contained subsoil in only nine plots of 738 sampled plots and gopher mounds contained subsoil in only one of 1272 plots (Hansen and Morris 1968). Subsequently, pocket gophers appear to be active mostly in surface soils. Near alpine treeline on Niwot Ridge, Colorado, mean bulk density of gopher-disturbed soils was significantly less than undisturbed intermound areas (Litaor et al. 1996). Lower soil density in gopher-disturbed areas may be responsible for larger daily soil temperature fluctuations and slightly lower soil moisture levels in disturbed soils than in the surrounding matrix as observed in southwest Georgia (Simkin et al. 2004). In addition to physical soil changes associated with pocket gopher activity, pocket gophers are also responsible for significantly altering the distribution of nutrients near burrows compared to undisturbed soils. Simkin et al. (2004) found that gopher mounds in Georgia had lower total carbon, nitrogen, ammonium, and phosphate than surrounding soils. Similar findings near alpine treeline on Niwot Ridge, Colorado, showed that gopher activity resulted in lower C, N, exchangeable Ca, and K in gopher mounds compared to

undisturbed areas. Conversely, Mielke (1977) found that P, K, and organic matter were higher in mounds than in intermound soils of the Uncompahgre Plateau, Colorado. Although discrepancies exist for whether gopher activity increases or reduces soil nutrients, Litaor et al. (1996) suggest that differences are likely the result of pre-disturbance soil conditions and disturbance history.

Differences in both physical characteristics and nutrient levels between gopher-disturbed and undisturbed soils have had substantial impact on vegetative communities. In the Sierra Nevada of California, sagebrush (*Artemisia rothrockii*) has expanded into montane meadows. Historically this advance was attributed to grazing and the reduction of herbaceous graminoids and forbs as well as increased aridity in grazed meadows. However, soil disturbance by gophers significantly increased sagebrush establishment in both meadows dominated by herbaceous species as well as meadows dominated by mixed sage-herb communities. Sagebrush seedling establishment was highest in gopher-disturbed areas within herbaceous dominated, mesic meadows and no seedlings emerged in herbaceous meadows free of gopher disturbance (Berlow et al. 2002). In northern Arizona, aspen (*Populus tremuloides*) preferentially grow in mountain meadows containing deep soils. However, in the presence of pocket gophers (*Thomomys bottae*), aspen are confined to rocky soils that are less conducive to pocket gophers and subsequently reduce gopher herbivory on aspen roots (Cantor and Whitham 1989). Forbis et al. (2004) examined nutrient redistributions and vegetation surrounding abandoned burrows and discovered that long abandoned burrows facilitated forb and fescue establishment. In alpine tundra communities of Niwot Ridge, Colorado, forbs buried by gopher activity recovered faster than graminoids or cushion plants.

Subsequently, forbs dominate alpine meadows in which gopher activity is high (Sherrod et al. 2005). In Washington, Larrison (1942) noted that gopher mound soils were aerated, rock-free, and supported yellow pine (*Pinus ponderosa*) seedlings with occasional Douglas-fir (*Pseudotsuga taxifolia*) and white fir (*Abies grandis*) seedlings. At alpine treeline it has been suggested that burrowing animals, such as pocket gophers, may facilitate conifer seedling establishment by exposing mineral soil and enhancing soil moisture and providing protection from wind (Holtmeier and Broll 2009). It is improbable, however, that all gopher-related changes to soil characteristics are beneficial to vegetation. Although gopher disturbances may aid vegetation in some environments, it has also been suggested that hardened gopher eskers may be too dense for some conifer seedling establishment (Zeng et al. 2007) and that burrowing mammals may gnaw and girdle conifer seedlings and result in high conifer mortality (Holtmeier and Broll 2009). Furthermore, not all ecosystems appear to respond equally. In Georgia, pocket gopher (*Geomys pinetis*) mounds in longleaf pine and wiregrass savanna had no significant influence on pine or grass germination and the authors suggested that future gopher disturbance-biotic response be conducted in other ecosystems (Simkin et al. 2004).

Some debate exists as to the impact of pocket gophers on conifers. In California, mountain pocket gophers (*Thomomys monticola*) were cited as a detriment to red fir (*Abies magnifica*) establishment. Gophers smothered small seedlings with excavated mound debris and consumed seedlings that grew within centimeters of burrow openings. Moreover, gopher tunnels exposed seedling roots to air and resulted in high seedling mortality (Tevis 1956). In the Pacific Northwest, gophers have been detrimental to ponderosa pine and Douglas-fir in both natural and planted forests (Capp 1976; Crouch

1969). In reforested areas of south-central Oregon, ponderosa, Jeffrey, and lodgepole pine seedlings and saplings all experienced mortality associated with pocket gopher activity (Crouch 1971). Conversely, in the mountains of Colorado, Schütz (2005) reported no evidence of northern pocket gopher activity associated with seedling mortality. Preliminary observations from my study sites in GNP are consistent with Schütz. Differences in gopher impacts on conifers may be due to the species of gopher (*Thomomys monticola* in the Pacific Northwest and *Thomomys talpoides* in the Rockies) as well as the conifer species (pines and Douglas-fir in the Pacific Northwest and subalpine fir in the Rockies).

In addition to the well-documented impacts gophers have on ecosystems as ecosystem engineers, the geomorphic effect of gophers has also undergone substantial research. In Colorado, Hansen and Morris (1968) noted that pocket gophers moved gravel-sized rocks to the ground surface and speculated that increased decomposition of the gravel would result in increased soil formation. It is important to note that smaller particle sizes from disintegrating gravel are more susceptible to subsequent erosional processes. On the Wasatch Plateau in Utah, Ellison (1946) estimated that pocket gopher spoils covered 3.5% of the area and deposited soil on the surface at a rate between 11.0-14.5 tons per hectare per year. In the Colorado Front Range, pocket gophers were suggested to be the dominant geomorphic agent in the alpine zone (Thorn 1978). Burns (1979) observed that approximately 35% of pocket gopher spoils were eroded annually for an average surface lowering of 0.0037 cm per year. By comparison, Burns stated that fluvial and eolian erosion only accounted for an average surface lowering of 0.0001 cm yr⁻¹. Sherrod and Seastedt (2001) examined pocket gopher (*Thomomys talpoides*)

burrows in Colorado and found soils disturbed by gophers to be more easily eroded by wind and water and Knight (2009) concluded that pocket gophers in Washington resulted in substantial soil movement and may be responsible for maintaining biodiversity in the area. On Niwot Ridge, lower bulk density and drier soil conditions of gopher mounds increased the potential for eolian erosion and past research found that the volume of one gopher mound decreased by 56.50% in less than three months (Litaor et al. 1996).

Although only gophers and marmots are discussed in this manuscript, it is important to note that the physical and chemical soil characteristics, as well as the impacts on plant communities, wrought by fossorial mammal activity is not confined to these species. Similar studies exist for pika (*Ochotona*) in Mongolia, Tibet, and the Himalaya (Bagchi et al. 2006; Wesche et al. 2007; Xinghu et al. 2007). Zokor (*Myospalax fontanierii*) mounds in Asia have been found to contain increased organic carbon in soils (Wang et al. 2008), increased temperature and nitrogen in disturbed soils (Zhang et al. 2003), and increased plant species diversity near abandoned burrows (Wang et al. 2008).

Acting either as zoogeomorphic agents or as ecosystem engineers, pocket gophers have a considerable impact on local environments. Gophers prepare sediment for erosion by wind and water, have impacts on adjacent plant communities, and gopher burrows create disturbance upon the landscape that are important for vegetation (Figure 4; Davis et al. 1991; Hobbs and Mooney 1991).



Figure 4. Pocket gopher eskers at Divide Peak, Glacier National Park, Montana. Eskers are created during winter months when gophers tunnel through snow and line tunnels with soil. Upon snowmelt in the spring, eskers collapse onto the remaining soil surface, desiccate, and begin to disintegrate.

Marmots

Much ecosystem engineering research has been conducted on marmot (*Marmota*) burrows around the world (Figures 5 and 6). In Russia, Tadzhiev and Odinoshoiev (1987) found that marmot activity redistributed soil nutrients and moisture, and modified the textural characteristics of the soil. Conversely, a study by Swihart and Picone (1994) in Connecticut found that soil pH and moisture of marmot-disturbed areas were not different from the surrounding undisturbed area. The impact of marmot disturbance on

vegetation has suggested that marmots reduce grasses and forbs near burrows (Barash 1989). del Moral (1984) stated that Olympic marmots (*Marmota olympus*) reduced palatable subalpine vegetation surrounding burrows while non-palatable vegetation increased, and Choler (2005) claimed that a reduction of one plant species due to marmot consumption facilitated establishment of another plant species (Figure 5). In agricultural fields, English and Bowers (1994) established that marmots were capable of altering vegetation characteristics over great distances. The authors determined that vegetation near marmot burrows contained less species richness and richness increased with distance from burrows. Although the number of burrows covered only a small proportion of the entire field, the influence was evident over a much broader area. Similar results have been found in the Alps with alpine marmots (*Marmota marmot*; Semenov et al. 2001; Semenov et al. 2003).

From a zoogeomorphic perspective, less is known about the impact of marmots. Tadzhiyev and Odinoshojev (1987) stated, in addition to that mentioned above, that marmots in the Tien Shen and Pamirs “form the microrelief” of the high-altitude region. Plaster (2003) found that yellow-bellied marmots in the Elk Mountains of Colorado were capable of moving a minimum of $2.69 \text{ m}^3 \text{ km}^{-2}$ annually. Moreover, Plaster noted two localized mass wasting events that may have been directly associated with marmot activity. In the Olympic Mountains, Olympic marmots generally burrow in open meadows and create distinctive downslope “porches” comprised of excavated earth and rock debris (Figures 6 and 7). Porches generally increase in size during summer months as marmots actively enlarge burrows. As stated above, sedges appear to grow well on

and around Olympic marmot porches because of disturbed soil, regular fertilization, and minimal grazing (Barash 1989).



Figure 5. Active Olympic marmot burrow in Olympic National Park, Washington. Notice the marmot sitting on the burrow porch as well as the modified meadow vegetation surrounding the burrow.



Figure 6. Olympic marmot burrow in Olympic National Park, Washington. For reference, the pink plastic of the flagging measures 6.35 cm high by 8.9 cm wide.



Figure 7. Olympic marmot burrow. Note the 50 mm camera lens cap for scale. Olympic National Park, Washington. Photo by David R. Butler.

Despite numerous studies on fossorial mammal activity, particularly those on pocket gopher and marmot burrows, none have examined the impact of abandoned burrows on conifer seed germination and seedling establishment at alpine treeline. Given that conifers at alpine ecotones are commonly used as proxies of climate change, a better understanding of the relationship between fine scale processes such as animal burrows and conifer location is needed to ensure that treeline ecotones are more accurately used as proxies of change. Furthermore, many of the controls of treeline are related and it is

important to identify the impact of individual factors. A review by Grace et al. (2002) examined past studies of treeline, with special emphasis on European locations, and stated that much evidence suggested an increase in elevation and tree establishment during periods of increased summer temperatures, but many theories and hypotheses of environmental controls co-varied and the authors suggested experimental discrimination was needed to identify the impact of individual factors. Körner (1998) also identified the need for experimental research to identify the control of individual variables on treeline. Detailed analysis of gopher and marmot disturbances and experimental research may provide the discrimination necessary to identify the importance of animal disturbances in treeline dynamics.

CHAPTER 3

STUDY SITES GEOGRAPHY

Glacier National Park

Glacier National Park, located in northwestern Montana, was initially protected as a forest reserve in 1897 and later established as a national park in 1910 (Glacier National Park 2002 as cited in Fagre 2003). In 1932 GNP was combined with adjacent Waterton National Park in southwestern Alberta, Canada, to become the first International Peace Park. GNP consists of 0.4 million ha that encompass the western Livingston and eastern Lewis mountain ranges and is bisected by the Continental Divide (Butler 1986b, 1989; Walsh et al. 1992; Butler et al. 2007). Mount Cleveland, the highest peak in the park, rises to 3191 m. During the Pleistocene, the area was heavily glaciated as evidenced by the northeast-southwest trending U-shaped valleys, many of which are occupied by finger lakes (Butler 1979). Because of its national park status, anthropogenic activity within park boundaries is limited and the park has become a focal point for climate change and natural environmental systems research (Hall and Fagre 2003; Bekker 2005; Resler and Tomback 2008).

Climate

The bisection of GNP by the Continental Divide results in two major climate types within the park, a modified maritime climate west of the Continental Divide and a more continental climate east of the Divide (Hansen 1948; Arno and Hammerly 1984). Moist, Pacific air masses dominate the western half of GNP and result in both heavy snowfall and precipitation with increased precipitation correlated with increased elevation. Along the Continental Divide, precipitation totals of 2500 mm have been recorded (Finklin 1986). In comparison, the eastern portion of GNP is cooler and relatively drier with precipitation totals averaging 585 mm annually (Finklin 1986; Butler et al. 1992; Walsh et al. 1992). East of the Continental Divide, GNP is dominated by a continental climate regime. The mountains of GNP have been described as having an intermountain climate because both coastal and continental climates are present (Mock and Birkeland 2000; McClung and Schaerer 2006).

Temperature and precipitation changes over the past several hundred years have enacted many environmental changes throughout the park. Increased global temperatures since the 1850s to the present have been cited as the cause of diminishing glaciers during the time period (Hall and Fagre 2003). Precipitation in the form of snow has been shown to be highly correlated with Pacific Decadal Oscillation (Zhang et al. 1997). When the index was negative, the Pacific Northwest and the northern Rocky Mountains received more precipitation in the form of snow and has been suggested to have an impact on regional vegetation (Alftine et al. 2003; Peterson and Peterson 2001; Peterson et al. 2002).

Vegetation

Tree species comprising alpine treeline in GNP are heavily controlled by climatic variables and differ on the west and east sides of the Continental Divide. West of the Divide, treeline species consist of Engelmann spruce (*Picea engelmannii*), subalpine larch (*Larix lyallii*), and subalpine fir (*Abies lasiocarpa*; Walsh et al. 1992). East of the Divide, treeline species are more reminiscent of the southern Rocky Mountains and include limber pine (*Pinus flexilis*), whitebark pine (*Pinus albicaulis*), and subalpine fir (Butler 1979; Walsh et al. 1992; Malanson and Butler 1994). Treeline in GNP is located at approximately 2000 m (Butler 1979; Arno and Hammerly 1984). Above treeline, the tundra environment is a diverse mosaic of tundra vegetation and rock. Tundra vegetation is dominated by the prostrate shrubs white dryas (*Dryas octopetala*) and netleaf willow (*Salix reticulata*), as well as the sedges northern singlespike sedge (*Carex scirpoidea*), and alpine bistort (*Polygonum viviparum*; Lesica and McCune 2004). Subalpine meadows at the lower threshold of the alpine treeline ecotone are commonly occupied by subalpine fleabane (*Erigeron peregrines*), glacier lily (*Erythronium grandiflorum*), and black alpine sedge (*Carex nigricans*; Hartley 2000).

Geology, Geomorphology, and Soils

The geology of GNP is complex and many comprehensive reviews exist. In-depth discussion of park geology is beyond the scope of this dissertation and readers are directed to the cited works and the references therein (Harris 1975; Rowe 1977; Harris and Kiver 1985). Despite the complex nature of GNP geology, it is important to highlight several components that affect local geomorphology and soils as well as

vegetation. Six distinct rock formations of marine origin are easily identifiable in GNP. They include the following formations, Altyn (magnesian or dolomitic limestone), Appekunny (argillite), Grinnell (argillite), Siyeh (limestone), Shepard (limestone), and Kintla (argillite; Harris 1975; Rowe 1977). During the late Cretaceous period to the early Eocene epoch, the Laramide Orogeny resulted in excessive folding and faulting inasmuch that older Precambrian strata (Altyn, Appekunny, Grinnell, Siyeh, Shepard, and Kintla) in the northern portion of the park was thrust overtop Cretaceous strata that formed under a shallow sea approximately 100 million years ago. The Cretaceous formations were not deeply buried and did not develop into strong rock like that of the Precambrian strata. Subsequently, when glaciers developed during the Pleistocene, the weak Cretaceous formations were easily eroded and resulted in the striking glacial landscape present today (Harris 1975; Rowe 1977; Harris and Kiver 1985).

The juxtaposition of hard Precambrian strata and weak Cretaceous material have created many interesting landforms and are susceptible to many current geomorphic processes. Butler et al. (1986) noted that two large rockfall events within the last 100 years were associated with the Lewis Overthrust. The abundant Precambrian and Cretaceous sediments have resulted in many debris flows that have been suggested to be controlled by storms and antecedent moisture conditions (Wilkerson and Schmid 2003). As mentioned above, debris flows, and rockfalls have a substantial impact on vegetation at treeline (Butler and Walsh 1994).

The soils of GNP are a result of the underlying geology. The argillites and limestones eventually weather into fine-grained loamy and silty soils (Veseth and Montagne 1980; Dutton and Marrett 1997). Soils between 1524 and 2896 m typically

develop into alpine meadow soils, which are dominated by well-drained loam or silt loam surface layers, gravelly or sandy loam subsoils, and fractured bedrock below. Alpine meadow soils occur in glacially-scoured cirques and on mountain slopes and usually develop into deeper soils in moist areas and shallower colluvial soils in drier sites. Minor inclusions in alpine meadow soils consist of rock outcrops, talus, and wet mineral soils in depressions and adjacent to tarns and mountain streams (Dutton and Marrett 1997). Soils underlying tree fingers extending into the alpine tundra reveal no significant difference from soils above alpine treeline and do not appear to react differently to climatic change (Schmid 2004).

Study Sites

Based on reconnaissance fieldwork, two sites in GNP will be studied to assess the proposed hypotheses; (1) Divide Peak, and (2) Preston Park (Figure 8). Both sites are located east of the Continental Divide in the Lewis Range.

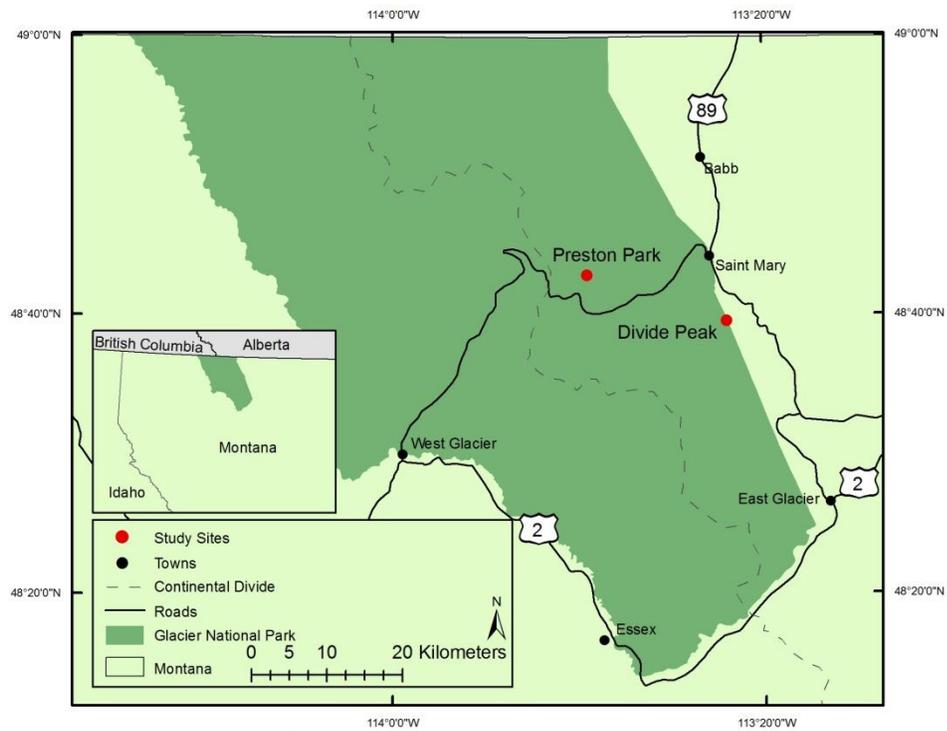


Figure 8. Study sites in Glacier National Park, Montana.



Figure 9. Divide Peak study site, Glacier National Park, Montana.

Divide Peak (Figure 9) is an isolated mountain on the eastern border of GNP. Much of the mountain slopes are dominated by mass wasting processes such as rockfall and rock avalanches. With a decrease in elevation, alpine tundra with isolated tree islands gives way to closed canopy forest over a short distance and limited elevational range. Active miniature patterned ground is common at Divide Peak (Sawyer 2007; Butler et al. 2009), but no patterned ground will be included in the study.

Preston Park (Figures 10, 11, and 12) is located in a northeast-southwest trending hanging glacial valley immediately east of the Continental Divide. The north and south

slopes of the valley experience active mass wasting events that commonly extend into the forest ecotone and reduce the elevation of treeline. Preston Park has some linear forest patterns (Butler et al. 2003) and is a heterogeneous landscape of subalpine meadows and conifers. A small tarn near the cirque headwall feeds a small stream that flows through the study area. All sample sites will be located away from the stream.



Figure 10. Preston Park, Glacier National Park, Montana.



Figure 11. Typical gopher-disturbed meadow in Preston Park, Glacier National Park, Montana.



Figure 12. Detailed photograph of gopher disturbance in a meadow in Preston Park, Glacier National Park, Montana. The length of the tape shown in this image is 4.5 m.

Olympic National Park

Olympic National Park was initially established as a national monument in 1909 and obtained national park status in 1938. The park covers 0.36 million ha of the Olympic Peninsula in northwestern Washington. The majority of the Olympic Mountains are included within the park as well as an 80 km section of beach (Harris and Kiver 1985). Subsequently, the park encompasses a wide range of environments including

alpine tundra of the Olympic Mountains down to sea stacks and beaches of the Pacific Ocean (Harris 1977). Mount Olympus, the highest peak in the park, rises to 2432 m.

During the Pleistocene, continental ice sheets advanced toward the Olympic Mountains but did not shape the current park. The ice sheet bifurcated with one arm extending west through the current Strait of Juan de Fuca and the other extending south in the Puget Sound. Alpine glaciers during the Pleistocene and Holocene eroded the current U-shaped valleys that are common throughout the park (Harris 1977). The Olympic Peninsula was one of the last places explored and colonized by westward expansion in the lower 48 states (NPS n.d.). Indigenous peoples spent time near Hurricane Ridge and Obstruction Point (personal communication with K. Kwarsick) but Anglo explorers and settlers did not venture deep into the mountains. Lt. Joseph P. O'Neill, who explored the area from 1885-1890, suggested the mountains be preserved because he saw no other use for the rugged country. The Olympic Mountains were designated as a forest preserve in 1897, a national monument in 1909, and eventually a national park in 1938 (Warren 1982). The rugged mountains and dense vegetation, coupled with early preservation, constitute a relatively natural environment with low human impacts.

Climate

Similar to GNP, ONP is divided into two distinct climatic regions. The western slope of the Olympic Mountains in the southwestern region of the park receives between 3556 and 4242 mm of annual precipitation and supports a temperate rainforest (NPS 2011). By contrast, the northeastern slope of the mountain range is in a rain shadow and

only 427 mm of precipitation are recorded annually in the city of Sequim (Petersen et al. 1983). Despite extreme differences in precipitation, the temperatures on both the west and east slopes of the mountain range are similar. The Quinault Ranger Station (50 m elevation) on the southwest side of ONP has a mean January temperature of 3.3°C and a mean July temperature of 17.2°C. The Elwha Ranger Station (100 m elevation) located in the northeast of the park has a mean January temperature of 2.2°C and a mean July temperature of 16.9°C (Zolbrod and Peterson 1999).

Climatic change across the Pacific Northwest has resulted in environmental change in a variety of mountain ranges (Miller and Halpern 1988; Magee and Antos 1992; Rochefort et al. 1994). In the alpine regions of ONP this has resulted in tree establishment in xeric areas during periods of above average precipitation and in mesic areas during periods of below average precipitation (Woodward et al. 1995). Zolbrod and Peterson (1999) modeled climate change in the Olympic Mountains and simulated results suggested that an increase in temperature would alter dominant tree species, distribution and abundance, and biomass of high-elevation ecosystems in the mountain range.

Vegetation

The alpine treeline vegetation of ONP is strongly controlled by precipitation. Conifer species growing in high elevation, subalpine meadows on the mesic, west side of the mountains consist of mountain hemlock (*Tsuga merensiana*) and Pacific silver fir (*Abies amabilis*; Kuramoto and Bliss 1970; Woodward et al. 1995). In subalpine meadows on the eastern slope, subalpine fir dominates most aspects, with patches of

Pacific silver fir and mountain hemlock growing on some northern exposures (Fonda and Bliss 1969; Kuramoto and Bliss 1970; Woodward et al. 1995). Subalpine meadows in the rain shadow generally consist of heath/ shrub communities on north aspects and grass/forb communities on south aspects with Idaho fescue (*Fescuta idahoensis*) being the dominant species (Kuramoto and Bliss 1970; Belsky and del Moral 1982). According to Zolbrod and Peterson (1999), the subalpine meadow-forest ecotone is controlled by microclimate and topography and is abrupt in nature.

Geology, Geomorphology, and Soils

Compared to the mountains of GNP, the geologic history of the Olympic Mountains is very young and is divided into two stages. During the Eocene epoch, the western slope of the Olympic Mountains was created by submarine lava flows. Sandstone and siltstone were deposited during the late Eocene and then no sedimentation occurred for approximately 16 million years. Sedimentation resumed in the Miocene epoch and tectonic stress resulted in much faulting, tilting, and overturning (Harris 1975; Rowe 1977; Harris and Kiver 1985). Beginning in the same epoch, the northeastern slope of the mountains developed a series of formations; Crescent (pillow basalt with sandstones, siltstones, and argillite), Aldwell (marine siltstone and sandstone), Lyre (conglomerate and sandstone), and Twin River (sandstone, schist, and siltstone, siltstone and basaltic boulders, siltstone, mudstone, and claystone; Harris 1975). The core of the Olympic Mountains have been highly sheared and folded because of tectonic activity and are a complicated combination of basalt, argillite, volcanic breccias, and metamorphic rock (Harris 1975; Rowe 1977; Harris and Kiver 1985).

The current landforms of the Olympic Mountains were developed by fault-controlled drainage which produced deeply incised valleys and glacial landforms created during glacial episodes (McNab and Avers 1994). On Olympic Mountain ridgetops, soil creep has been cited as an important erosional agent (Tabor 1971). Hansen-Bristow and Price (1985) noted the presence of turf-banked terraces in alpine environments of the northeastern Olympic Mountains. Substantial rock avalanches, suggested to be caused by earthquakes, were documented over the past 1000 years but no rock avalanches in the past 100 years have been shown to be associated with storms or earthquakes (Schuster et al. 1992). Undoubtedly, mass wasting events have an impact on alpine treeline in ONP, despite the lack of scientific studies to validate this claim.

Soils of subalpine meadow (grass and sedge) and forest (subalpine fir) around Hurricane Ridge in northeastern ONP consist of Typic Dystricrypts below meadow vegetation and Lithic Dystricrypts below conifer vegetation (Prichard et al. 1999). Dystricrypt soil profiles consist of strong organic matter in the A horizon, a weak B horizon, and distinct deeper mineral horizons (Soil Survey Staff 1988; Prichard et al. 1999).

Study Sites

Study sites in ONP were determined by previous research and the presence of abandoned marmot burrows. Previous work by Griffin and colleagues (2008, 2009) documented the location of abandoned burrows and provided sampling locations within the park. Although Olympic marmots exist in alpine environments in all areas of the park, three sites in the northeastern section of ONP are chosen for analysis (Figure 13).

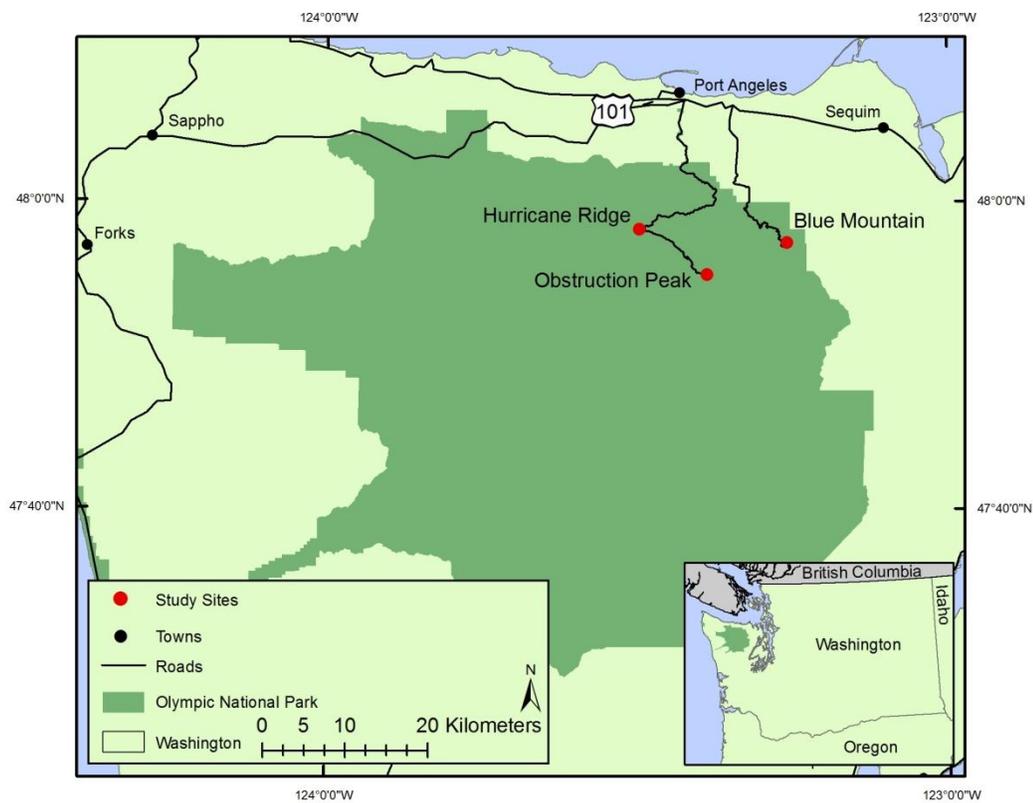


Figure 13. Study sites in Olympic National Park, Washington.

Blue Mountain (Figure 14) is in the northeastern-most part of ONP. The geology of the region is primarily sandstone and argillite with pockets of basalt, conglomerate, and pebbly sandstone (Tabor and Cady 1978). Up to elevations of approximately 1067 m, large granitic glacial erratics mark the elevational extent of the Cordilleran ice sheet (USGS 2004). The north and west sides of the mountain are covered by a mosaic of conifers and subalpine meadows, whereas the east and south sides are covered by substantial alpine and subalpine meadows with some rock outcrops present. Abandoned marmot burrows exist in the alpine meadows of the eastern slope above treeline.

Hurricane Hill (Figure 15) is located approximately 2.5 km northwest of the Hurricane Ridge Visitor Center. The geology of the hill and surrounding area is primarily sandstone and argillite with areas of slate and basalt (Tabor and Cady 1978; USGS 2004). An east-west trending ridge west of Hurricane Hill is heavily forested on the north aspect and comprised of alpine meadows with some tree islands and individual trees as well as some subalpine meadows further downslope. During reconnaissance fieldwork, many marmots were seen foraging near the summit of Hurricane Hill, and both active and abandoned burrows exist in alpine meadows along the ridge.



Figure 14. Blue Mountain study site, Olympic National Park, Washington.



Figure 15. Hurricane Hill study area, Olympic National Park, Washington. Notice how active rockfall from the cliffs on the right has suppressed the upward advancement of trees.

Obstruction Point (Figures 16 and 17) is located approximately 12 km southeast of the Hurricane Ridge Visitor Center. The geology of the Obstruction Point region is primarily slate and sandstone but some pillow basalt also exists (Tabor and Cady 1978; USGS 2004). Late-lying snow is common near Obstruction Point and many abandoned marmot burrows are buried by seasonal snowpack in late July and early August in years of above average annual snowfall. Accessible burrows were found in alpine meadows above treeline and in some cases in subalpine meadows immediately below treeline.



Figure 16. Obstruction Peak study site, Olympic National Park, Washington.



Figure 17. Subalpine meadow undergoing conifer invasion near Obstruction Point in Olympic National Park, Washington.

Similarities and Differences Between Study Sites and Parks

Both Glacier and Olympic National Parks consist of rugged mountains with alpine and subalpine meadows and tundra vegetation at treeline. Although the two parks are separated by great distances and one is clearly more continentally located than the other, both parks have areas of similar climate. The northeastern portion of Olympic National Park is located in the rain shadow of the Olympic Mountains and has a climate similar to that of the continental mountains of eastern Glacier National Park. The

underlying substrate of the study areas in both GNP and ONP is primarily sandstone, siltstone, and argillite and both parks have substantial mass wasting at treeline. In both northeastern ONP and eastern GNP, the dominant conifer species at treeline surrounding the study sites is subalpine fir. Climatically, geomorphically, and vegetatively, all study sites are remarkably similar (Table 1). The differences that exist between parks are primarily those associated with subalpine and alpine vegetation and the dominant fossorial mammal at treeline. As stated above, GNP alpine tundra vegetation is dominated by white dryas, netleaf willow, northern singlespike sedge, and alpine bistort. In subalpine and alpine meadows, the dominant vegetation is subalpine fleabane, glacier lily, and black alpine sedge. Subalpine and alpine meadows in ONP are dominated by Idaho fescue. The primary difference between the study sites in GNP and ONP is that of fossorial mammal. GNP has extensive gopher disturbance on many upland slopes at these sites.

Table 1. Elevational ranges, aspects, parent material, dominant treeline species, and climatic variables of study sites in both Glacier National Park, Montana and Olympic National Park, Washington. Note the surprisingly similarity between all study sites.

	<i>Glacier National Park</i>		<i>Olympic National Park</i>		
	Divide Peak	Preston P.	Blue Mtn.	Hurr. Rg.	Obst. Pt.
Elevation Range (m)	2133-2164	2116-2206	1707-1808	1493-1646	1737-1798
Aspect	SSE-SE	SW	SSE-SE	SSW-SW	S-SSW
Parent Material	Limestone	Glacial till	Sandstone and argillite	Sandstone and argillite	Slate and Sandstone
Dominant Treeline Species	Subalpine fir w/ Whitebark pine	Subalpine fir	Subalpine fir	Subalpine fir	Subalpine fir
Mean Annual Precip (mm)	585 (St. Mary, MT)		427 (Elwha Ranger Station, WA)		
Mean July Temp (°C)	16.9		16.9		



Figure 18. Northern pocket gopher (*Thomomys talpoides*). Notice the claws that make this rodent a formidable digger. Photo by National Park Service.

In ONP, Olympic marmots (*Marmota olympus*) are common fossorial rodents throughout the alpine tundra and subalpine meadows. The animals are endemic to the Olympic peninsula and their range is almost entirely restricted to the Olympic Mountains. Current research has noted that Olympic marmot populations are in decline and an estimated 2000 exist in their natural habitat (Griffin et al. 2008; Griffin et al. 2009). Olympic marmots are substantially larger than pocket gophers. Average male and female body lengths are 740 mm and weights vary depending on pre- or post-hibernation measurements (Figure 19). Typical hibernation occurs over 7-8 consecutive months during winter months. Average pre- and post-hibernation weight of both males and females is 8.2 and 3.6 kg respectively (Barash 1973). *Marmota olympus* reside in colonies occupying many (13-79) burrows (Barash 1989; Edelman 2003). Large burrows with many entrances are used as sleeping dens and many other shallow (120-180 cm deep) burrows with single entrances are used as latrines and refuge from predation (Beltz and Booth 1952; Barash 1973). Excavated burrow material is deposited downslope and develops into a fan shaped “porch” averaging 0.8 m² (Barash 1973). Marmots are commonly seen resting on porches and using them as lookouts. Unlike the debate between gophers and conifer mortality, little is known about Olympic marmot effects on conifers. Subalpine fir and western white pine (*Pinus monticola*) have occasionally been gnawed (Barash 1973; Wood 1973 and Watson 1976 as found in Edelman 2003) but no additional research exists.



Figure 19. Olympic marmot (*Marmota olympus*) in Olympic National Park, Washington. Photo by Hilary Whitesides.

Despite spanning the extent of the alpine ecotone, different processes have been shown to control treeline dynamics in subalpine meadows near the edge of the closed canopy compared to dynamics at higher elevations where trees transition into tundra. In meadow environments, climatic variables greatly influence treeline dynamics. For example, in xeric meadows, conifers benefitted from increased summer precipitation and temperature (Jakubos and Romme 1993) and cool, wet summers have been shown to enhance tree establishment in meadow environments (Rochefort and Peterson 1996).

Additional results indicated that wet meadows had more establishment under drier climatic conditions and the opposite was true for dry meadows (Woodward et al. 1995). Similar to subalpine meadows, it has been noted that tree dynamics at the upper end of the ecotone are also related to temperature and precipitation (Butler et al. 1994; Hessler and Baker 1997; Lloyd and Graumlich 1997; White et al. 1998; Fagre et al. 2003). Despite the controlling factor of climate on both ends of the ecotone, many topographic and geomorphic controls exist at both locations. Topographic convexities have been shown to facilitate and control treeline in meadow environments (Rocheport and Peterson 1996; Butler et al. 2003) but the upper-end of the alpine treeline ecotone appears to be more prone to topographic and geomorphic control than the lower extent of the ecotone. Winter desiccation has been partly attributed to topographic variables at treeline (Cairns 2001) and solifluction and nurse rocks have been shown to favor seedling establishment (Butler et al. 2004; Resler et al. 2005; Resler 2006, see Whitesides and Butler 2011, and references therein, for more examples of treeline dynamics ranging from the lower to upper extents of the alpine treeline ecotone). Therefore, although the study sites represented in this study range from the lowest elevations of the ecotone (meadows near the edge of closed canopy forest) to the highest (tree island environment) and may be affected by different processes, this study attempts to assess the ubiquitous nature of fossorial mammal disturbance throughout the entire alpine ecotone environment.

The similarities between National Parks and study areas allows for the control of climate, substrate, and some aspects of vegetation. The differences in fossorial mammals enable this research to compare and contrast gopher and marmot impacts on seedling establishment, and ultimately treeline dynamics, in separate regions of the United States.

CHAPTER 4

METHODS

Field Sampling

To assess the hypotheses listed above, fieldwork in the aforementioned study sites was conducted. In GNP, previous reconnaissance indicated that gopher activity was extensive in both subalpine meadows and meadows at treeline, but little if any gopher activity was noticeable in the alpine tundra. Based on a pilot study conducted in 2009, subalpine meadows with gopher disturbance at the lowest extent of the alpine treeline ecotone were randomly selected in Preston Park. Effort was made to match local site characteristics such as slope and aspect when selecting disturbed meadows. Three meadows with similar local characteristics and levels of gopher disturbance were chosen for sampling. Three undisturbed meadows were also selected for evaluation. Undisturbed meadows were also randomly selected, but ultimately, only locations with similar local site characteristics were chosen. Undisturbed sites contained no visual evidence of gopher activity. Undisturbed areas did, however, contain small areas of exposed rocky substrate, felled trees, juvenile trees, etc. which have been identified as important features for the establishment of conifer species in the extreme environment of the alpine ecotone (Resler et al. 2005; Resler 2006). To ensure that these non-mammal-related features were not excluded from the analysis, sampling occurred on or adjacent to nurse features when randomly selected as sample locations. The same procedures were

applied at Divide Peak where both disturbed and undisturbed subalpine meadows near treeline were randomly selected and evaluated. To ensure equal sampling within meadows, the long and short axes of each randomly selected meadow were measured, and the meadows were divided into three equal quadrats. Within each quadrat, 10 random points were sampled. A blind toss of a transect pin determined sampling locations (Resler and Tomback 2008). In gopher disturbed areas, the esker nearest the blind toss was sampled. The same stratified random sampling procedure occurred in undisturbed meadows.

Because of the declining nature of Olympic marmot populations and restrictions enacted to protect the mammal, sampling in ONP was not random. The NPS expressed concern that my research may be detrimental to Olympic marmots so at their request, I contacted Suzanne Cox-Griffin and received the location of known abandoned marmot burrows in the northeastern portion of ONP. Abandoned burrow sites provided by Cox-Griffin were sampled within the study sites listed above. To sample undisturbed areas, a blind toss of a transect pin indicated an azimuth upon which a transect was extended from the burrow disturbance to a distance of 10 m, where a sample was taken in the undisturbed matrix (Swihart 1991). If the azimuth from the blind toss resulted in a sampling location within 10 m of another abandoned burrow, the procedure was repeated until a successful undisturbed location was sampled.

At all disturbed and undisturbed sites, a variety of samples and tests were collected and performed (Table 2). First, soil surface temperature was recorded with an infrared thermometer. Sampling occurred in most areas between the hours of noon and 4pm to standardize the effects of diurnal heating and measure soils at their warmest

temperatures. Past research has indicated that soil surface temperatures may be important to conifer germination. High surface temperatures (40-50°C) at alpine treeline have been recorded in the mountains of central Mexico (Lauer and Klaus 1975), and Holtmeier and Broll (2010) stated that high soil surface temperatures may reduce germination and limit seedling advancement. Therefore, it was necessary to identify soil surface temperature both on mammal-disturbed sites and on undisturbed sites to assess the impact burrow disturbance may have on surface temperatures. Subsurface temperatures were recorded with a soil thermometer at a depth of 10 cm at all disturbed and undisturbed locations (Canals et al. 2003). Schütz (2005) stated that the temperature regime at a depth of 5-10 cm may approximate seed bed conditions for conifer seedlings. In snow glades of Colorado, vegetation acted as an insulator and resulted in increased sub-surface temperatures when compared to non-vegetated snow glades (Schütz 2005). Low sub-surface temperatures may preclude germination as shown with spruce seeds (Patten 1964). Gopher and marmot disturbances may have reduced vegetative cover and may result in larger sub-surface temperature fluctuations that are detrimental to seedling establishment.

At all locations, soil moisture was recorded at 10 cm below the surface with a Lincoln soil moisture meter that measures relative soil moisture compared to saturated soil (Freestone and Harrison 2006; Dendy and Li 2010). Soll (1994) found that fuel moisture and seedling mortality of subalpine fir in ONP were negatively correlated across four different vegetative communities. This correlation will be assessed on animal-disturbed soils.

As shown by Butler and Butler (2009) and Knight (2009), gopher eskers are significantly less compact than neighboring soils. A pocket penetrometer was used to record soil compaction rates (in triplicate) on disturbed and undisturbed substrates. Every fifth sample, a soil probe was used to collect soil from the top 10 cm of the soil horizon (Inouye et al. 1987; Canals et al. 2003). Approximately 135 cm³ of soil were collected from each study site. All soil samples were allowed to air dry and were taken to Utah State University's analytical laboratories for physical and chemical analysis.

Finally, seedlings within the study sites, as well as trees near the edge of the meadows, were examined for signs of peeling (Schütz 2005) that may be attributed to gopher and marmot herbivory. In Douglas-fir plantations of the Pacific Northwest, 30% of plantation seedlings were damaged by animal activity, but only 4% of the 30% was attributed to pocket gophers (Black et al. 1979). Schütz (2005) noted that no gopher herbivory on seedlings was present in his study in the Colorado Front Range. It is important to determine if gophers or marmots directly impede seedling establishment in disturbed areas through herbivory impacts.

Table 2. The purpose of each study method. Note that each method satisfies at least one research objective (O1-O4) of this study. Data collection methods, supporting literature, and sampling procedure are also highlighted.

Purpose	Method	Literature	Procedure
Fulfills O1 and O2	Pocket penetrometer	(Butler and Butler 2009; Knight 2009)	Take triplicate measurements of soil compaction on disturbed soils and on the undisturbed surrounding matrix.
Fulfills O1 and O2	Surface and subsurface soil temperature	(Lauer and Klaus 1975; Holtmeier and Broll 2010; Schütz 2005)	Take soil temperature data at soil surface and 10 cm below the surface
Fulfills O1 and O2	Soil moisture	(Soll 1994)	Measure soil moisture 10 cm below soil surface
Fulfills O1, O2, and O3	Soil collection	(Sherrod and Seastedt 2001; Gutiérrez and Jones 2006)	Collect soil samples using a soil probe and analyze in a laboratory setting.
Fulfills O3 and O4	Collect site data	(Buckner 1977; Forbis et al. 2004; Schütz 2005; Bagchi et al. 2006)	Observe herbivory effects on seedlings, conifer species, age, etc.
Fulfills O3 and O4	Experimental growth in a controlled setting	(Poorter and Remkes 1990; Körner 1998; Grace et al. 2002)	Grow dominant conifer seed on disturbed and undisturbed substrates

Laboratory Analysis

Soil samples from the same area (e.g. Preston Park, Divide Peak, etc.) and the same type (e.g. disturbed or undisturbed) were combined to create a representative and sufficiently large sample for accurate soil testing (Staben et al. 2003; Texas A&M University n.d.). The samples were tested for pH, salinity, texture, P, K, and percent organic matter. Percent organic matter, rather than loss-on-ignition, was used to evaluate

organic matter. Previous research has shown that samples from my study sites often result in elevated levels of calcium carbonate, which may overestimate carbon in loss-on-ignition tests (Resler 2004).

Soil not destroyed in the soil testing was used to compare seed germination in disturbed and undisturbed soils. The average soil compaction observed in the field for gopher and marmot disturbed soils, as well as average soil compaction for adjacent undisturbed sites of both Glacier and Olympic National Parks, was recreated with sampled soils in Stuewe and Sons' 'cone-tainers' (Figure 20). The growth experiment was conducted in Logan, UT, beginning in late August and extending through early October. Although Logan, UT, is located further south than both GNP and ONP, the average daily solar radiation during September in Logan is similar to the average daily received at the parks during the months of July (Figures 23 and 24). Therefore, the growing conditions in Logan can be assumed to be representative of growing conditions within the national parks during the peak growing season.

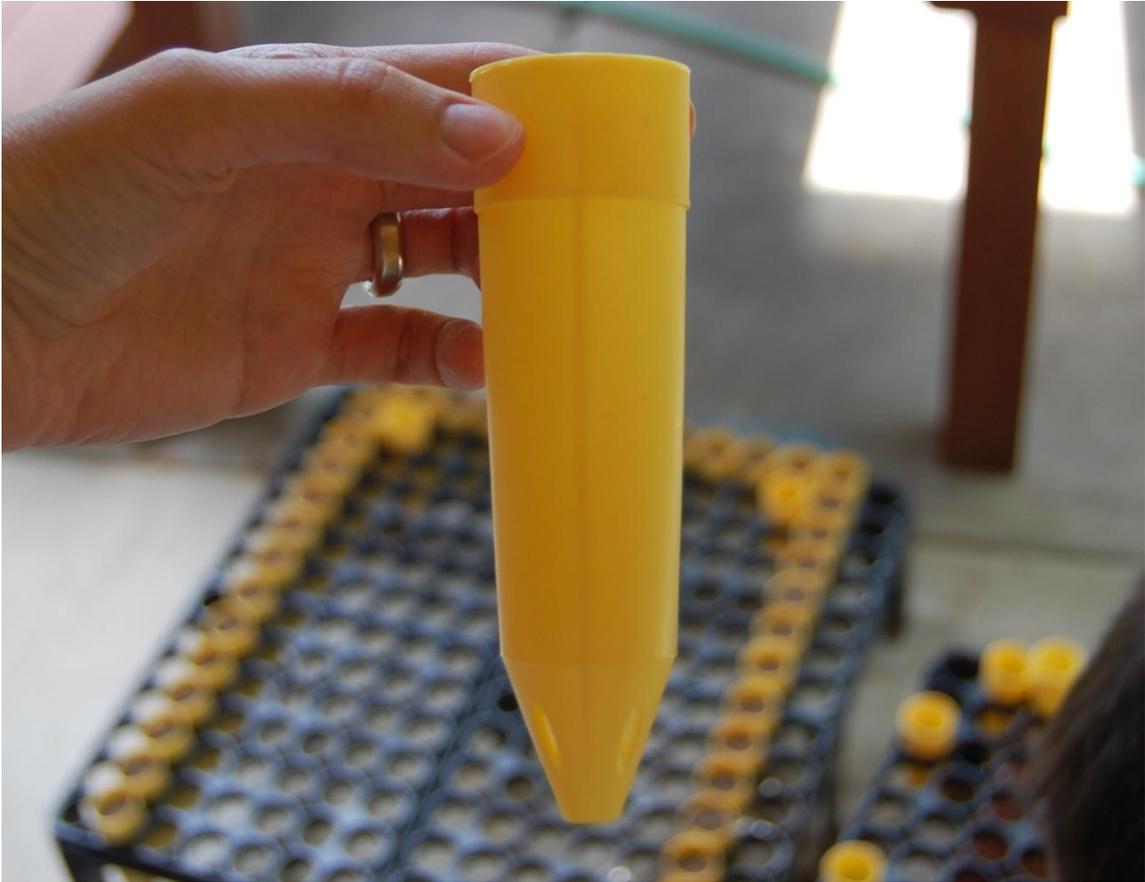


Figure 20. Stuewe and Sons' 'cone-tainer'. The cone-tainer measures 14 cm in length and has a diameter of 3.8 cm. Each cone-tainer holds up to 115 cm³ of soil.

The recycled, biodegradable, polypropylene cone-tainers were 14 cm in length and had a diameter of 3.8 cm. Each cone-tainer was capable of holding 115 cm³ of soil. Thirty-five cm³ of vermiculite was placed in the bottom of each cone-tainer to prevent soil from escaping through water drainage holes in the bottom of the cone-tainer. The remaining 80 cm³ of cone-tainer volume was filled with soil from each study site and compacted to field-observed soil compaction with a wooden tamping device. Subalpine fir seeds (98% purity and 98% cut germination), collected from the San Isabel National Forest of central Colorado, were purchased from Sheffield's Seed Company. Seed

collection from the study sites in Glacier and Olympic National Parks was not feasible, so an external seed source was used in order to standardize bias. Seeds were scarified by saturation for 24 hours in distilled water and then cold stratified at 2° C for 34 days to break seed dormancy (Anderson and Winterton 1996; USDA 2008). Fully imbibed seeds were planted at a depth of 6.4 mm (Sheffield's Seed Co.) in each prepared cone-tainer in order to assess seed germination controlled by soil compaction. Planting at a depth of 6.4 mm was not an unrealistic aberration of the natural environment within the national parks. The heterogeneous nature of micro-scale soil topography may enable many seeds to settle into small fissures and, therefore, meet the specific requirements for seed germination (Harper et al. 1965).

In addition to soils collected in GNP and ONP, seeds were planted in typical greenhouse control soil, which was used as a control to evaluate differences in compaction. Each prepared cone-tainer was randomly placed within a Steuwe and Sons holding tray specifically designed for cone-tainer experiments (Figure 21). Three runs, consisting of five replications of each soil type, were planted at two-day intervals. Three runs of the data were used to reduce the likelihood of erroneous outcomes caused by differences in climatic variables on the day of planting as well as other uncontrollable exogenous factors. All runs were hand-irrigated after planting until soils were saturated. The samples were allowed to dry to levels found in the field, after which additional irrigation occurred with a timed sprinkling system to ensure uniform distribution of water among runs and replications. Samples were again allowed to dry and then were irrigated. This wet-dry cycle is consistent with late spring and summer precipitation caused by thunderstorms which have been observed as common meteorological phenomena

throughout the national parks of western North America (Finklin 1986; Butler 1990; Butler and Malanson 1996; Meyer and Pierce 2003). A portable weather station recorded air temperature for the duration of the experiment. Samples were allowed to germinate for two months (Ashton et al. 1998; Kennedy and Sousa 2006). The average temperature during this period, as recorded by the portable weather station was 17.8°C (Figure 22). This temperature is less than one degree warmer than July average temperatures for the study sites within the sample national parks. At the end of the 8-week period, all samples were carefully excavated, examined under a binocular microscope, and compared to the USDA's *The Woody Plant Seed Manual* (2008) to determine the extent of germination.

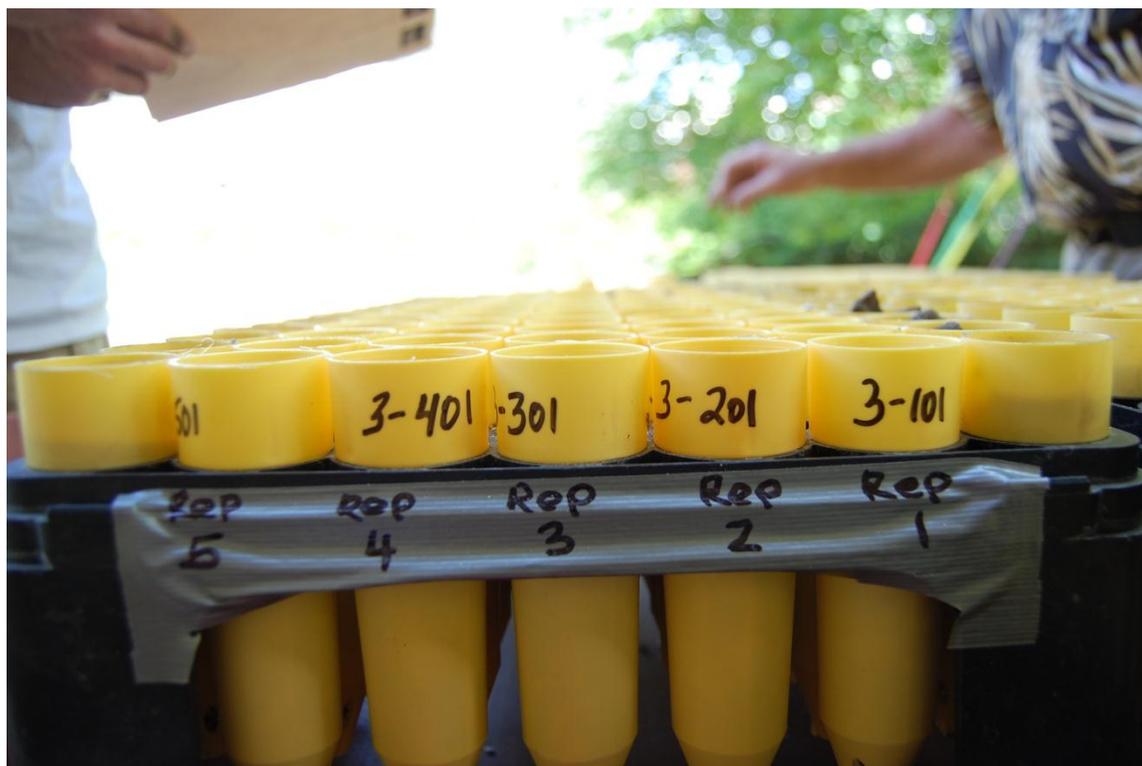


Figure 21. All cone-tainers were placed in holding trays and three runs of five replications were performed.

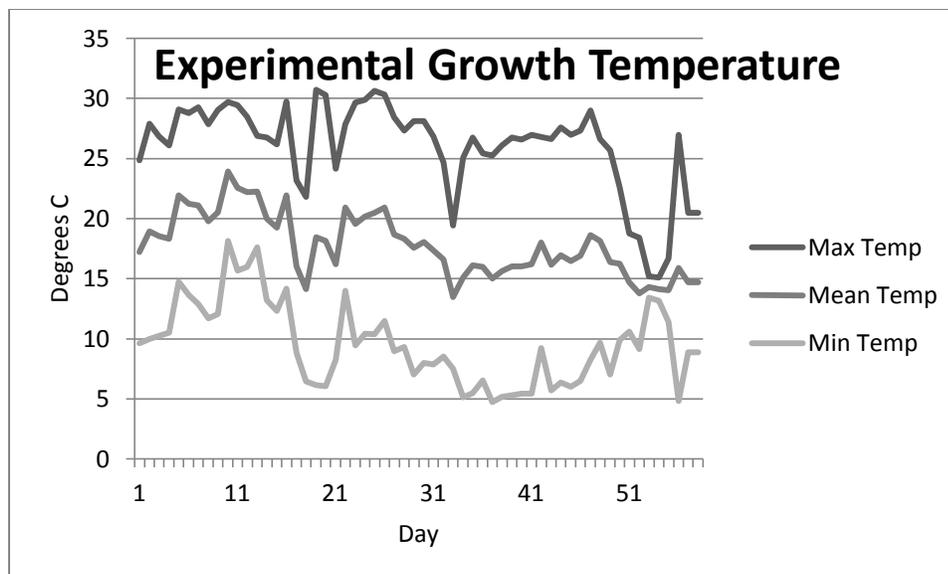


Figure 22. Temperature data collected with a portable weather station at the site of cone-tainer experimental growth. Day 1 was 16 August 2011 and day 58 was 12 October 2011. The mean temperature for the growing period was 17.8 degrees.

Average Daily Solar Radiation Per Month

JULY

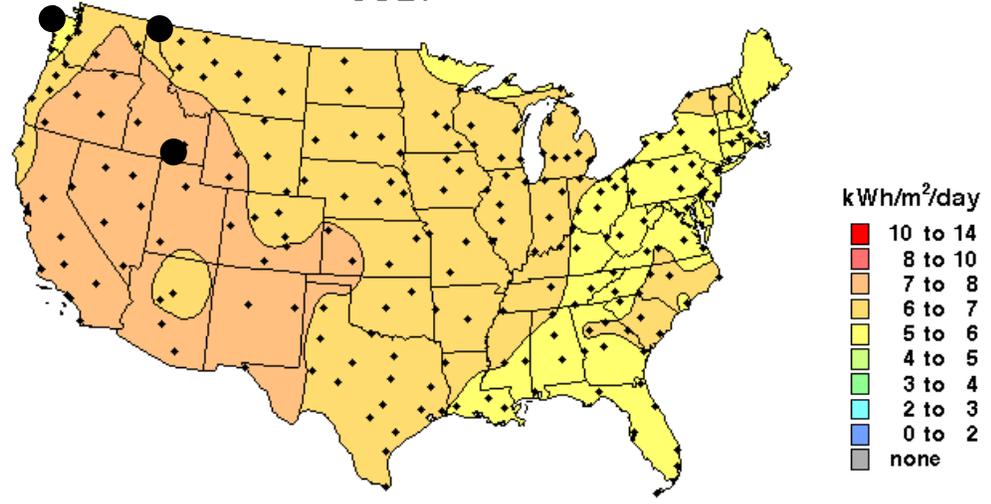


Figure 23. Average daily solar radiation for the month of July. Notice that both Glacier National Park, Montana, and Olympic National Park, Washington, receive less solar radiation than Logan, Utah, during the month of July. Small black dots represent locations where solar radiation was recorded. Large black dots represent Glacier and Olympic National Parks as well as Logan, Utah. This map represents averages and does not depict local variability. Source: National Renewable Energy Laboratory.

Average Daily Solar Radiation Per Month

SEPTEMBER

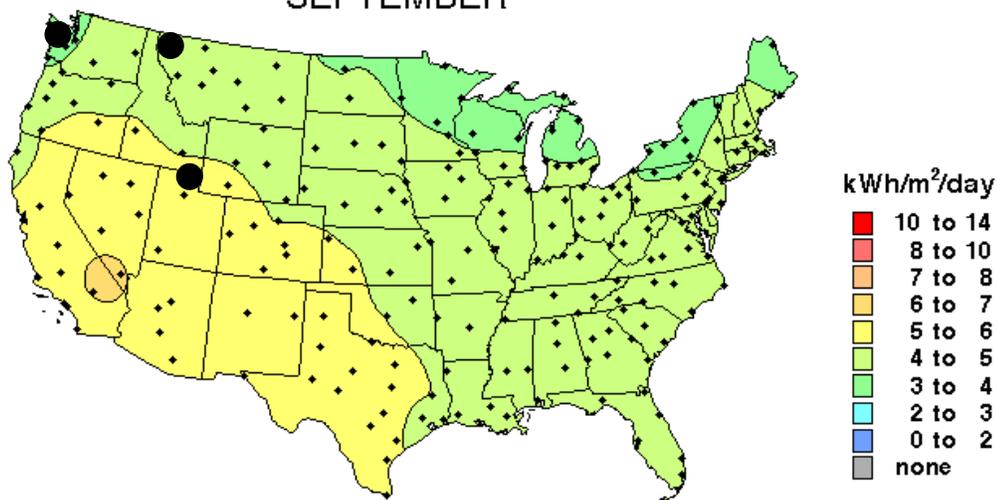


Figure 24. Average daily solar radiation for the month of September. Notice that both Glacier National Park, Montana, and Olympic National Park, Washington, receive less solar radiation than Logan, Utah, during the month of September and that September radiation in Utah is similar to July radiation received at the national parks. Small black dots represent locations where solar radiation was recorded. Large black dots represent Glacier and Olympic National Parks as well as Logan, Utah. This map represents averages and does not depict local variability. Source: National Renewable Energy Laboratory.

Statistical Analysis

As is common with biological variables, most of the data collected did not meet the assumptions of normality based on the Kolmogorov-Smirnov test. The more conservative, non-parametric statistical methods, therefore, were used to determine significant differences between the physical characteristics of disturbed sites and the characteristics of the surrounding matrix. To assess the sub-local scale hypothesis (H_01) that physical soil characteristics are the same in undisturbed and mammal-disturbed sites

within study areas, the Wilcoxon matched pairs test was implemented. Because samples at the sub-local scale were drawn from the same area and were expected to have related characteristics, a matched pairs test was appropriate. Statistical significance was determined by an alpha of 0.05. Where statistical differences were observed, the Friedman test was used to analyze differences within sample sites and between disturbed and undisturbed soils at a given location. Where the Friedman test was used, Wilcoxon tests and the Bonferroni correction were used as posthoc tests. In all cases where the Bonferroni correction was employed, the level of statistical significance was reduced to 0.0167. The Bonferroni correction, in recent years, has received criticism when applied to ecological research (Moran 2003; García 2004). It has been stated that the Bonferroni correction increases the likelihood of rejecting a null hypothesis when it would be incorrect to do so. Despite these criticisms, published primarily as opinion or forum articles, research at arctic and alpine treeline consistently use Bonferroni corrections to assess statistical significance (Gamache and Payette 2005; Bader et al. 2007; Danby and Hik 2007; Batllori and Gutiérrez 2008; Alvarez et al. 2009; Batllori et al. 2009; Batllori et al. 2010). Ultimately, it has been stated that the Bonferroni correction is a viable method of determining statistical significance but the method is not a panacea for posthoc tests (Cabin and Mitchell 2000). The same Friedman test with Wilcoxon and Bonferroni correction procedures were appropriate to examine the local scale hypothesis (H_02) that physical soil characteristics are the same in undisturbed areas and areas of mammal disturbance.

The landscape scale hypothesis (H_03) that no difference exists in physical soil characteristics between Preston Park, GNP, and Divide Mountain, GNP, was analyzed

with the Mann-Whitney test (Elliot and Kipfmueller 2011). The distance between study sites, as well as the differences in soil parent material, warranted the use of independent statistics at this scale because no related assumptions were expected or known. The same method was used to assess differences between Hurricane Ridge, ONP, Blue Mountain, ONP, and Obstruction Point, ONP. The Mann-Whitney test was also employed to examine the regional scale hypothesis (H_04) that no difference between physical soil characteristics exists between GNP and ONP. Similar to the landscape scale approach, no apparent relation existed between national parks and independent tests were the appropriate choice (Elliot and Kipfmueller 2011).

Because soil testing required the aggregation of multiple soil samples to perform adequate analysis, too few samples were generated to obtain reliable statistical testing. Therefore, the null hypothesis (H_05) stating that chemical soil characteristics are the same between locations of mammal-disturbed and undisturbed areas within a study area was examined in a more qualitative format.

Chi-square (X^2) is a non-parametric test that compares observed data counts with expected values. This method was used to test the null hypothesis (H_06) that standardized temperature and precipitation would result in similar seed germination at all scales, independent of soil compaction. The chi-square test specifically tests the probability that if soils were similar between undisturbed and mammal-disturbed sites, observed germination would be consistent with expected germination values. Soil moisture data, as mentioned above, was measured at the ordinal level and consequently, the non-parametric correlation test, Kendall's Tau, was required to determine if correlations existed between physical soil characteristics. Furthermore, the high number

of tied ranks associated with the soil moisture data made Kendall's Tau the most appropriate test for assessing correlation.

CHAPTER 5

RESULTS

Field Sampling

Sub-local Scale

The sub-local scale examines differences in undisturbed and disturbed soils sampled within the same area (e.g. Preston Park, Divide Mountain). The sub-local scale was able to be examined within study sites in GNP, but was unable to be assessed in ONP. The restrictions imposed by the NPS and the accompanying non-random sampling in designated areas, did not allow for multiple sampling sites to exist within Hurricane Ridge, Blue Mountain, and Obstruction Point. Subsequently, the sub-local scale analysis is only presented for sites in GNP.

Three undisturbed sites were sampled in Preston Park, GNP, and the sampling results are highlighted in Table 3. Preston Park Site A consisted of a typical subalpine meadow located at the lower limit of the alpine treeline ecotone. The meadow is dominated by glacier lilies and is surrounded by mature subalpine fir trees. Four subalpine fir seedlings (less than 20cm) were observed in the meadow and no evidence of herbivory was noted on the seedlings nor on the more mature trees surrounding the meadow. Preston Park Site B contained more herbaceous cover than Site A. Glacier lilies dominated the meadow in most locations and one side of the meadow contained several false hellebore plants. A slight slope existed across the meadow and false

hellebore was located at the lower edge of the slope. Higher soil moisture values were recorded toward the false hellebore than toward the opposite end of the meadow where the surrounding vegetation was dominated by mature subalpine fir trees. One seedling was observed growing in the meadow (< 20cm) and was growing in close proximity to a small, partially exposed boulder. Again, no evidence of girdling by gophers was evident on the seedling or on the surrounding trees. Preston Park Site C, although dominated by glacier lilies, contained more fescue cover than the other two sites. The meadow also contained more exposed surface rock than the other two sites. Surrounding vegetation consisted of subalpine firs which showed no evidence of gopher herbivory. No seedlings were present in the meadow. All data at undisturbed sites were collected under clear skies with an air temperature ranging from 24-27°C.

Table 3. Data for undisturbed sites within Preston Park, Glacier National Park, Montana.

Comp = Soil compaction measured in kg/cm^2

SubTemp = Subsurface soil temperature ($^{\circ}\text{C}$) measured at 10cm below the soil surface.

SurfTemp = Surface soil temperature ($^{\circ}\text{C}$).

Moist = Moisture measured on a scale from 0-10 where 0 is completely dry and 10 is saturated soil.

Glacier National Park Preston Park Undisturbed soils Preston Park Site A				
	Comp	SubTemp	SurfTemp	Moist
n	30	30	30	30
\bar{x}	2.01	16.60	29.36	-
M	1.92	15.00	28.70	1.00
s	0.45	4.26	4.19	-
Min	1.25	12.00	23.80	0.00
Max	3.50	28.00	41.20	4.00
Range	2.25	16.00	17.40	4.00

Preston Park Site B				
	Comp	SubTemp	SurfTemp	Moist
n	30	30	30	30
\bar{x}	1.87	10.90	31.15	-
M	1.79	11.00	33.25	6.00
s	0.33	1.37	8.26	-
Min	1.42	8.00	13.30	1.00
Max	2.83	14.00	45.50	10.00
Range	1.42	6.00	32.20	9.00

Preston Park Site C				
	Comp	SubTemp	SurfTemp	Moist
n	30	30	30	30
\bar{x}	1.99	13.90	30.43	-
M	1.88	14.00	29.95	3.00
s	0.54	3.95	8.07	-
Min	1.00	8.00	17.60	0.00
Max	3.17	21.00	44.20	7.00
Range	2.17	13.00	26.60	7.00

Results from gopher-disturbed sites within Preston Park, GNP are summarized in Table 4. All gopher-disturbed sites in Preston Park were comprised of meadows containing a network of anastomosing gopher eskers. Atmospheric conditions during sampling at all sites were clear and ambient air temperature ranged from 21 to 27°C. No seedlings within gopher-disturbed sites showed evidence of girdling or herbivory. Mature trees surrounding disturbed sample sites were also free from visual gopher impacts. Specific details concerning the individual sites revealed that Preston Park Site X contained no seedlings within gopher disturbance, Site Y contained 3 subalpine fir seedlings (< 20cm) and Site Z contained 6 subalpine fir seedlings less than 20cm in height. All sites were representative of typical Preston Park meadows covered by glacier lilies and surrounded by subalpine fir trees.

Table 4. Data for gopher-disturbed sites within Preston Park, Glacier National Park, Montana.

Comp = Soil compaction measured in kg/cm^2

SubTemp = Subsurface soil temperature ($^{\circ}\text{C}$) measured at 10cm below the soil surface.

SurfTemp = Surface soil temperature ($^{\circ}\text{C}$).

Moist = Moisture measured on a scale from 0-10 where 0 is completely dry and 10 is saturated soil.

Glacier National Park Preston Park Gopher-disturbed Preston Park Site X				
	Comp	SubTemp	SurfTemp	Moist
n	30	30	30	30
\bar{x}	0.90	18.83	18.77	-
M	0.92	19.00	17.65	3.00
s	0.26	2.41	3.63	-
Min	0.42	15.00	13.30	2.00
Max	1.58	27.00	28.10	5.00
Range	1.17	12.00	14.80	3.00

Preston Park Site Y				
	Comp	SubTemp	SurfTemp	Moist
n	30	30	30	30
\bar{x}	0.68	9.60	21.22	-
M	0.67	9.00	20.30	2.00
s	0.26	1.57	8.72	-
Min	0.25	6.00	9.30	1.00
Max	1.25	14.00	38.90	3.00
Range	1.00	8.00	29.60	2.00

Preston Park Site Z				
	Comp	SubTemp	SurfTemp	Moist
n	30	30	30	30
\bar{x}	0.90	18.70	39.68	-
M	0.88	19.00	40.25	2.00
s	0.31	1.90	3.62	-
Min	0.42	14.00	30.00	1.00
Max	1.58	21.00	47.60	6.00
Range	1.17	7.00	17.60	5.00

Within Preston Park, GNP, there was no significant difference in soil compaction between the three undisturbed sites ($X^2(2) = 3.52, p = 0.172$; Figure 25). Gopher-disturbed soils, however, were statistically different from each other ($X^2(2) = 14.42, p < 0.001$). Wilcoxon tests and a Bonferroni correction were applied, thus reducing significance to the 0.0167 level, and differences in soil compaction were identified between Preston Park sites 2 and 3 ($T = 702.5, z = -3.16, r = -0.41$) as well as sites 3 and 5 ($T = 741.5, z = -2.58, r = -0.33$), but no difference existed between sites 2 and 5 ($T = 897, z = -0.27, r = -0.03$).

Subsurface soil temperatures on undisturbed soils of Preston Park revealed significant differences between the three sites ($X^2(2) = 33.53, p < 0.001$; Figure 25) with specific differences between Preston Park site A and Preston Park site B ($T = 485, z = -6.41, r = -0.83$) as well as between Preston Park site B and Preston Park site C ($T = 718.5, z = -2.94, r = -0.38$). There was no difference between Preston Park site A and Preston Park site C ($T = 759.5, z = -2.32, r = -0.30$). Similar findings existed in gopher-disturbed subsurface soil temperatures ($X^2(2) = 46.58, p < 0.001$) with differences existing between Preston Park sites 2 and 3 ($T = 485, r = -0.83$) and sites 3 and 5 ($T = 718.5, z = -2.94, r = -0.38$). There was no significant difference between sites 2 and 5 ($T = 759.5, z = -2.32, r = -0.30$).

On the soil surface, no difference existed in soil surface temperatures between undisturbed sites within Preston Park ($X^2(2) = 1.27, p = 0.531$; Figure 26). Gopher-disturbed soils, however, were significantly different ($X^2(2) = 45.27, p < 0.001$). Although Preston Park sites 2 and 3 were near the 0.0167 significance threshold, no significant difference existed ($T = 763.5, z = -2.24, r = -0.29$). Nor did differences exist

between sites 3 and 5 ($T = 898.5$, $z = -0.24$, $r = -0.03$), nor sites 2 and 5 ($T = 903.5$, $z = -0.17$, $r = -0.02$).

The soil moisture at the three undisturbed sites was very different ($X^2(2) = 31.79$, $p < 0.001$; Figure 26). Results from Wilcoxon tests identified that differences in soil moisture existed between all study sites (Preston Park sites 1 and 4 ($T = 515.5$, $z = -6.01$, $r = -0.78$), Preston Park sites 1 and 6 ($T = 592$, $z = -4.89$, $r = -0.63$) as well as Preston Park sites 4 and 6 ($T = 679$, $z = -3.53$, $r = -0.46$)). Similar findings from gopher-disturbed soils within Preston Park revealed differences in soil moisture between sites ($X^2(2) = 28.34$, $p < 0.001$), with specific differences between Preston Park sites 2 and 3 ($T = 633$, $z = -4.46$, $r = -0.58$) and between sites 2 and 5 ($T = 630$, $z = -4.50$, $r = -0.58$). There was no difference in soil moisture between Preston Park sites 3 and 5 ($T = 893.5$, $z = -0.36$, $r = -0.05$).

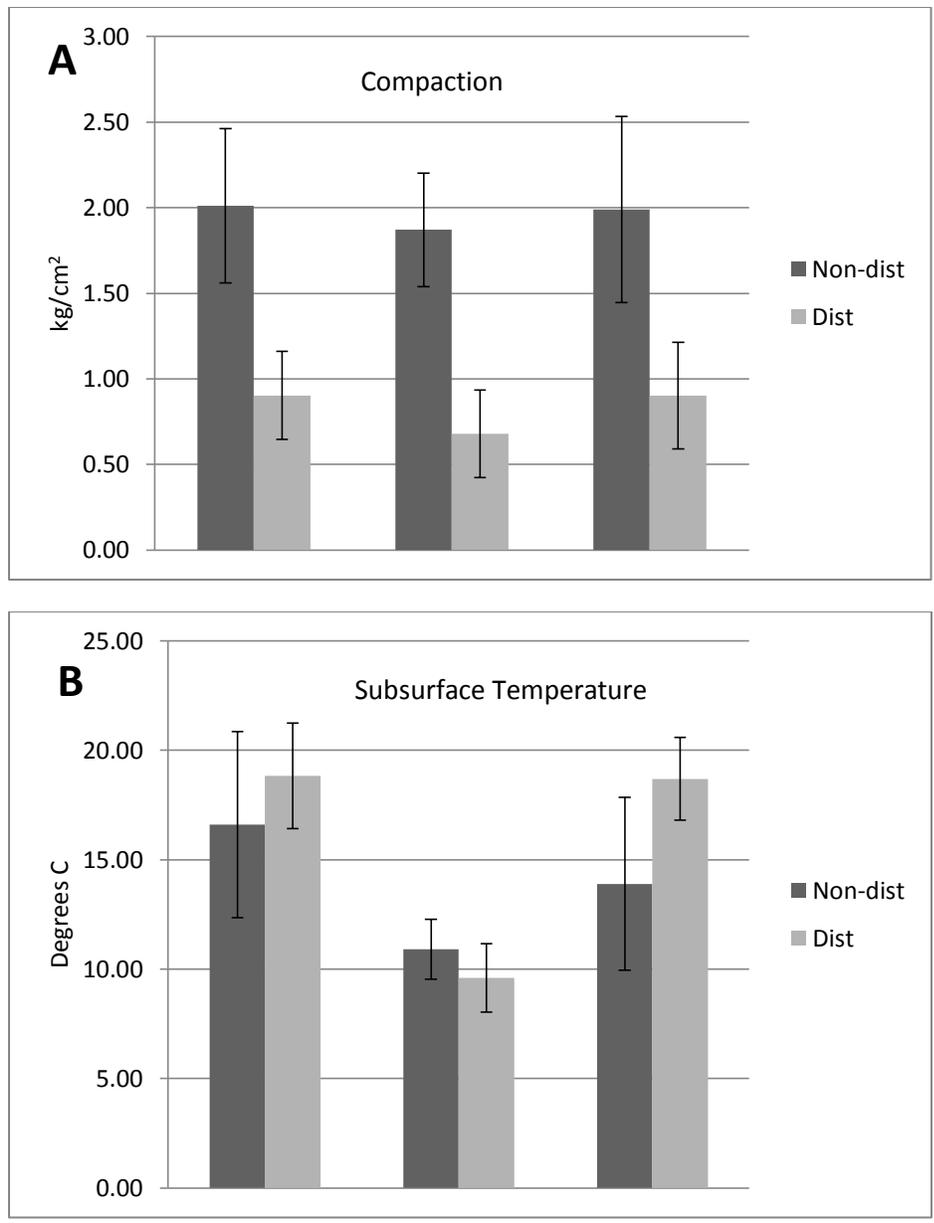


Figure 25. Soil compaction and subsurface temperature data from six sample sites within Preston Park, Glacier National Park, Montana. Dark grey bars represent undisturbed soils and light grey bars display gopher-disturbed soil data. Panel A shows the differences in soil compaction (kg/cm²) between undisturbed and disturbed soils and panel B displays subsurface soil temperatures (°C) on undisturbed and disturbed soils. Error bars display one standard deviation above and below the mean.

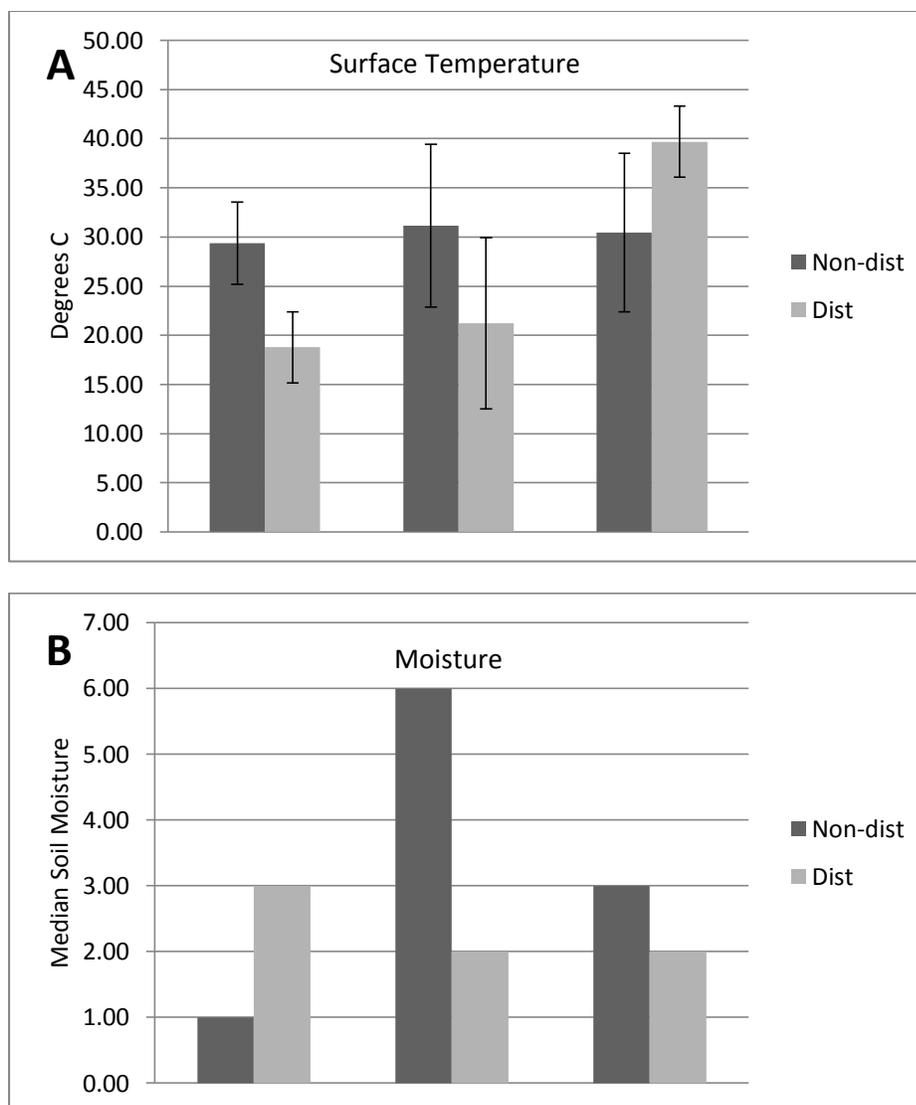


Figure 26. Surface temperature and soil moisture data from six sample sites within Preston Park, Glacier National Park, Montana. Dark grey bars represent undisturbed soils and light grey bars display gopher-disturbed soil data. Panel A exhibits soil surface temperatures ($^{\circ}\text{C}$) and panel B shows soil moisture measured on a scale from 0 to 10. Zero corresponds to dry soils and a value of 10 corresponds to saturated soils. Error bars display one standard deviation above and below the mean on soil temperature. No error bars were needed for ordinal data displayed in panel B.

Unlike Preston Park, which represents the lower elevation of the alpine treeline ecotone, Divide Mountain represents the upper limit of the ecotone. Two undisturbed and two gopher-disturbed sites were identified and sampled at this location. The proximity of the upper extent of the treeline at Divide Mountain to fine-scale turf-banked terraces and needle-ice pans (Sawyer 2007), which have been shown to influence conifer establishment (Resler et al. 2005; Resler 2006) prohibited sampling at additional sites. The two undisturbed sites at Divide Mountain are characterized by more herbaceous vegetative cover than Preston Park with some dryas present at the sites. Although the majority of the trees surrounding these locations were subalpine fir, several five-needle pines were present as well as the occasional spruce. Both sites contained a slight slope and atmospheric conditions were clear and the air temperature ranged from 24-28°C. Divide Mountain Site E contained no seedlings within the study site whereas Site F contained 1 subalpine fir seedling (< 20cm) and one smaller fir tree (< 40cm). Soils sampled from undisturbed sites contained few soil horizons. Specific results from undisturbed sites at Divide Mountain are found in Table 5.

Table 5. Data for undisturbed sites at Divide Mountain, Glacier National Park, Montana.

Comp = Soil compaction measured in kg/cm^2

SubTemp = Subsurface soil temperature ($^{\circ}\text{C}$) measured at 10cm below the soil surface.

SurfTemp = Surface soil temperature ($^{\circ}\text{C}$).

Moist = Moisture measured on a scale from 0-10 where 0 is completely dry and 10 is saturated soil.

Glacier National Park				
Divide Mountain				
Undisturbed				
Divide Site E				
	Comp	SubTemp	SurfTemp	Moist
n	30	30	30	30
\bar{x}	1.64	13.20	30.79	-
M	1.58	13.50	30.05	8.00
s	0.44	1.81	5.24	-
Min	1.00	10.00	19.90	2.00
Max	2.83	17.00	43.00	10.00
Range	1.83	7.00	23.10	8.00

Divide Site F				
	Comp	SubTemp	SurfTemp	Moist
n	30	30	30	30
\bar{x}	1.74	16.63	33.32	-
M	1.67	16.00	33.55	8.00
s	0.33	2.46	4.88	-
Min	1.17	11.00	24.60	4.00
Max	2.42	20.00	40.30	10.00
Range	1.25	9.00	15.70	6.00

Gopher-disturbed sites at Divide Mountain were almost identical in vegetation cover and dominant species compared to undisturbed locations (Table 6). Atmospheric conditions were also clear and air temperatures ranged between 25 and 29°C. Soil samples revealed no soil horizons in disturbed soils. The primary difference was the comprehensive network of gopher eskers in disturbed locations. As Site V, no seedlings were observed on disturbed substrate but several dead trees (< 40cm) were observed in close proximity to gopher disturbance. Visual examination showed no evidence of gopher herbivory on the dead standing stems, but subsurface herbivory was not evaluated. No girdling was apparent on living trees surrounding the gopher disturbance. Site W was slightly rockier than Site V, and limestone fragments were observed on the soil surface. No seedlings were present in the gopher-disturbed area and no evidence of herbivory was noted.

Table 6. Data for gopher-disturbed sites at Divide Mountain, Glacier National Park, Montana.

Comp = Soil compaction measured in kg/cm^2

SubTemp = Subsurface soil temperature ($^{\circ}\text{C}$) measured at 10cm below the soil surface.

SurfTemp = Surface soil temperature ($^{\circ}\text{C}$).

Moist = Moisture measured on a scale from 0-10 where 0 is completely dry and 10 is saturated soil.

Glacier National Park Divide Mountain Gopher-disturbed Divide Site V				
	Comp	SubTemp	SurfTemp	Moist
n	30	30	30	30
\bar{x}	1.12	10.23	20.80	-
M	1.17	10.00	20.95	8.50
s	0.39	1.96	7.31	-
Min	0.25	6.00	7.90	0.00
Max	1.83	14.00	36.40	10.00
Range	1.58	8.00	28.50	10.00

Divide Site W				
	Comp	SubTemp	SurfTemp	Moist
n	30	30	30	30
\bar{x}	0.93	19.63	36.18	-
M	0.75	20.00	36.00	10.00
s	0.47	3.45	4.69	-
Min	0.33	12.00	26.50	4.00
Max	2.08	26.00	46.00	10.00
Range	1.75	14.00	19.50	6.00

The differences between study sites at Divide Mountain contained some similarities to those observed within Preston Park but also revealed several differences. Analogous to Preston Park, soil compaction between undisturbed sites at Divide Mountain were not different ($T = 127.5$, $z = -1.48$, $p > 0.05$, $r = -0.19$; Figure 27). Unlike gopher-disturbed soil compaction at Preston Park, however, gopher-disturbed soils at Divide Mountain were not statistically different ($T = 156$, $z = -1.58$, $p > 0.05$, $r = -0.20$). Subsurface soil temperatures between undisturbed ($T = 2.5$, $z = -4.58$, $p < 0.001$, $r = -0.59$) and between gopher-disturbed sites ($T = 0$, $z = -4.79$, $p < 0.001$, $r = -0.62$) at Divide Mountain were significantly different and were consistent with findings from Preston Park (Figure 27). Soil surface temperatures at Divide Mountain were also consistent with Preston Park findings in that no difference existed between undisturbed soil surface temperatures ($T = 155$, $z = -1.59$, $p > 0.05$, $r = -0.21$), but a significant difference was present between soil surface temperatures on gopher-disturbed soils ($T = 10$, $z = -4.58$, $p < 0.001$, $r = -0.59$; Figure 28). Unlike Preston Park, soil moisture on undisturbed soils was not different between undisturbed sites at Divide Mountain ($T = 111$, $z = -1.13$, $p > 0.05$, $r = -0.15$), but similarly to Preston Park, significant differences in soil moisture existed between gopher-disturbed locations at Divide Mountain ($T = 88$, $z = -2.02$, $p < 0.05$, $r = -0.26$; Figure 28).

Because of limitations in the sampling design enforced by the National Park Service within ONP, comparisons at the sub-local scale were not possible on undisturbed and marmot-disturbed soils.

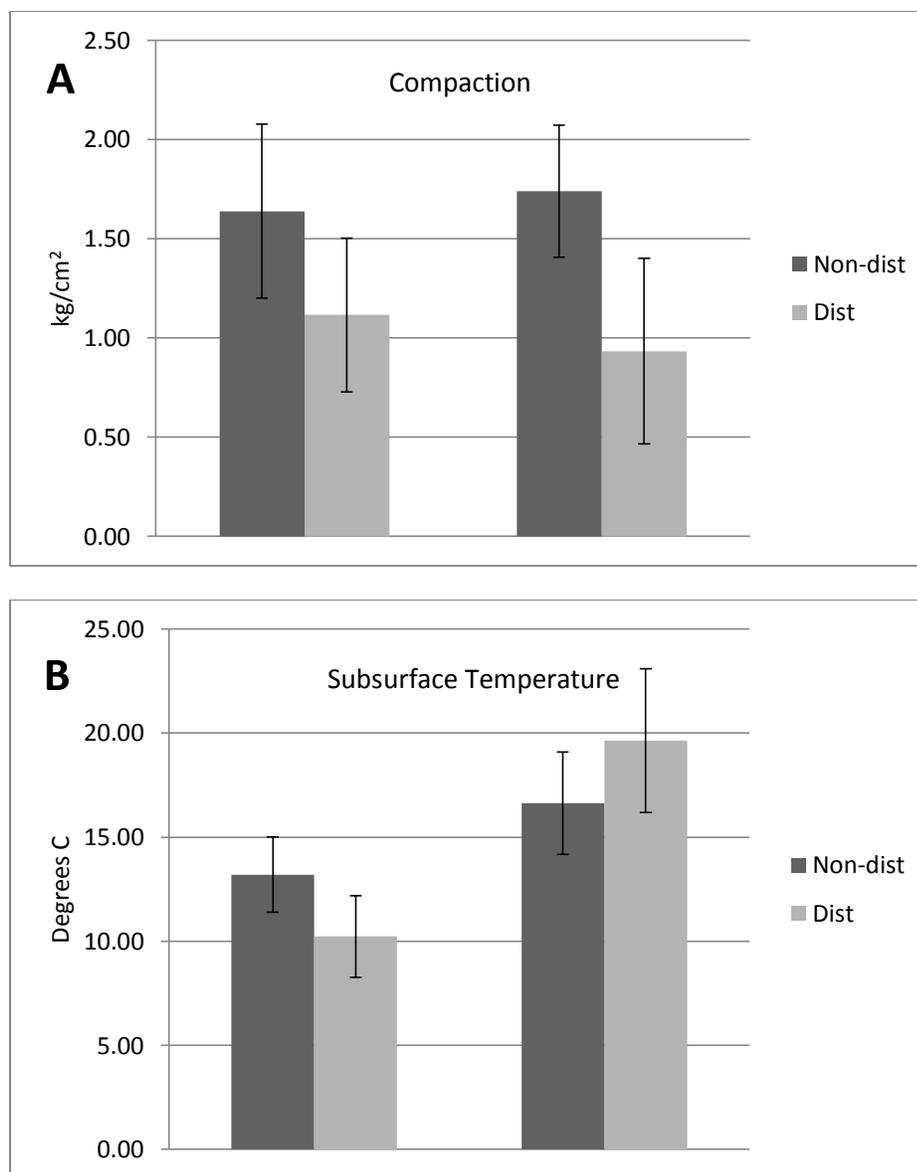


Figure 27. Soil compaction and subsurface temperature data from four sample sites at Divide Mountain, Glacier National Park, Montana. Dark grey bars represent undisturbed soils and light grey bars display gopher-disturbed soil data. Panel A shows the differences in soil compaction (kg/cm²) between undisturbed and disturbed soils. Panel B displays subsurface soil temperatures (°C) on undisturbed and disturbed soils. Error bars display one standard deviation above and below the mean.

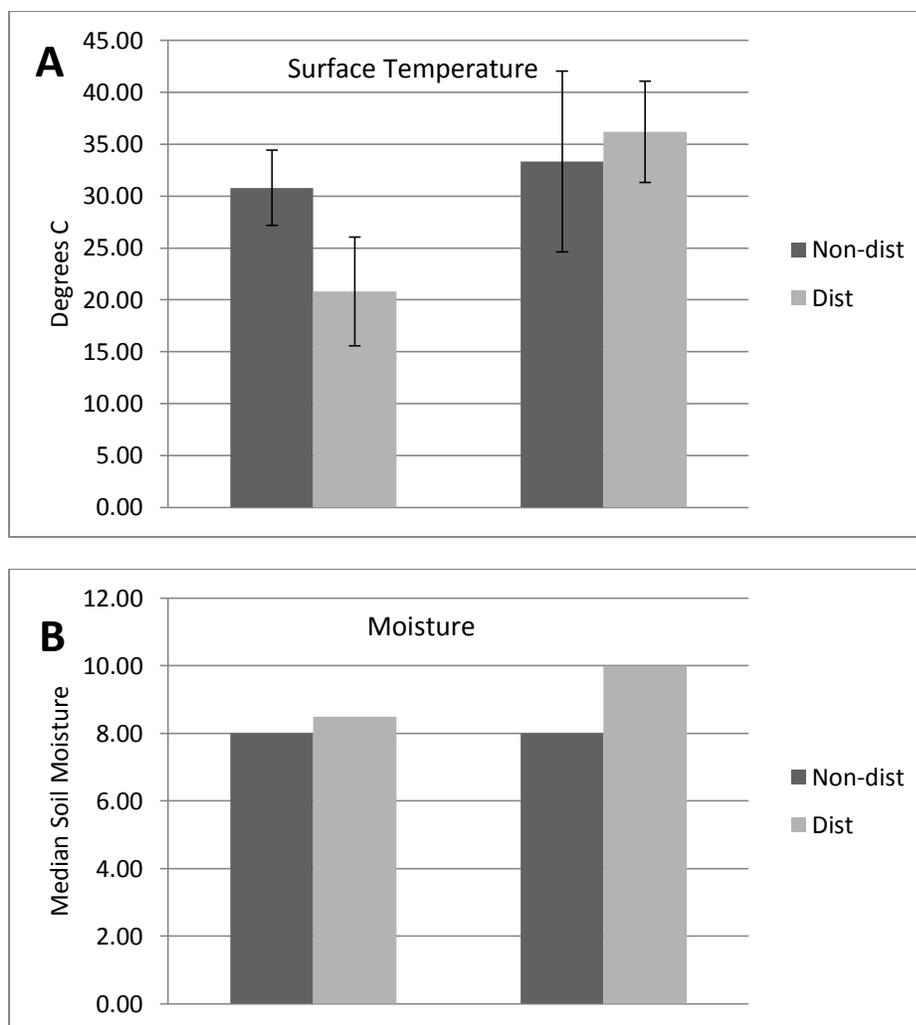


Figure 28. Surface temperature and soil moisture data from four sample sites at Divide Mountain, Glacier National Park, Montana. Dark grey bars represent undisturbed soils and light grey bars display gopher-disturbed soil data. Panel A exhibits soil surface temperatures ($^{\circ}\text{C}$) and panel B shows soil moisture measured on a scale from 0 to 10. Zero corresponds to dry soils and a value of 10 corresponds to saturated soils. Error bars display one standard deviation above and below the mean. No error bars were needed for ordinal data displayed in panel B.

Local Scale

The local scale examines the difference between undisturbed soils and disturbed soils at each site. In GNP, undisturbed soils were compared to gopher-disturbed soils at both Preston Park and Divide Mountain (Tables 7 and 8).

Undisturbed soils were significantly more compact ($M = 1.92$) than gopher-disturbed soils ($M = 0.75$), $T = 8.5$, $z = -8.16$, $p < 0.001$, $r = -0.61$. Comparable to Preston Park findings, undisturbed soils at Divide Mountain were significantly more compact ($M = 1.67$) than gopher-disturbed soils ($M = 1.00$), $T = 68.5$, $z = -6.09$, $p < 0.001$, $r = -0.79$ (Figure 29).

Undisturbed soils were significantly cooler ($M = 13^{\circ}\text{C}$) in the subsurface than gopher-disturbed soils ($M = 18^{\circ}\text{C}$) at Preston Park, $T = 923.5$, $z = -3.85$, $p < 0.001$, $r = -0.29$, but no significant subsurface temperature difference existed in undisturbed soils and gopher-disturbed soils at Divide ($T = 722.5$, $z = -0.17$, $p > 0.05$, $r = -0.02$; Figure 29). Soil surface temperatures in Preston Park on undisturbed soils were significantly warmer ($M = 31.2^{\circ}\text{C}$) than surface temperatures on gopher-disturbed soils ($M = 23.75^{\circ}\text{C}$), $T = 1387.5$, $z = -2.66$, $p < 0.05$, $r = -0.20$ (Figure 30). Analogous results exposed significantly warmer ($M = 31.65^{\circ}\text{C}$) temperatures on undisturbed soils than gopher-disturbed ($M = 29.50^{\circ}\text{C}$) soils at Divide, $T = 565$, $z = -2.58$, $p < 0.05$, $r = -0.33$.

Undisturbed soils at Preston Park were significantly more moist ($M = 3$) than gopher-disturbed soils ($M = 2$), $T = 867.5$, $z = -3.37$, $p < 0.001$, $r = -0.25$. At Divide Mountain, however, no difference existed in soil moisture between undisturbed and gopher-disturbed soils ($T = 559.50$, $z = -1.39$, $p > 0.05$, $r = -0.18$; Figure 30).

The physical soil characteristics observed on both undisturbed and gopher-disturbed soils did not function in isolation and many variables were correlated (Tables 9 and 10). On undisturbed soils in Preston Park, soil compaction was significantly correlated with both subsurface soil temperature and soil moisture. Soil moisture was also correlated with subsurface soil temperatures. On gopher-disturbed soils, significant correlations existed between subsurface soil temperature and both surface temperature and moisture. A correlation was also observed between moisture and surface temperature. At Divide Mountain, significant correlations existed between soil moisture and subsurface temperatures on undisturbed soils. Gopher-disturbed soils revealed more correlation between variables, with significant findings existing between soil compaction and surface temperature, surface and subsurface temperature, and surface temperature and moisture.

Table 7. Data comparing undisturbed soils to gopher-disturbed sites within Preston Park, Glacier National Park, Montana.

Comp = Soil compaction measured in kg/cm^2

SubTemp = Subsurface soil temperature ($^{\circ}\text{C}$) measured at 10cm below the soil surface.

SurfTemp = Surface soil temperature ($^{\circ}\text{C}$).

Moist = Moisture measured on a scale from 0-10 where 0 is completely dry and 10 is saturated soil.

Glacier National Park Preston Park Undisturbed				
	Comp	SubTemp	SurfTemp	Moist
n	90	90	90	90
\bar{x}	1.96	13.80	30.31	-
M	1.92	13.00	31.20	3.00
s	0.45	4.13	7.05	-
Min	1.00	8.00	13.30	0.00
Max	3.50	28.00	45.50	10.00
Range	2.50	20.00	32.20	10.00
Gopher-disturbed				
	Comp	SubTemp	SurfTemp	Moist
n	90	90	90	90
\bar{x}	0.83	15.71	26.56	-
M	0.75	18.00	23.75	2.00
s	0.29	4.77	11.02	-
Min	0.25	6.00	9.30	1.00
Max	1.58	27.00	47.60	6.00
Range	1.33	21.00	38.30	5.00

Table 8. Data comparing undisturbed soils to gopher-disturbed sites at Divide Mountain, Glacier National Park, Montana.

Comp = Soil compaction measured in kg/cm^2

SubTemp = Subsurface soil temperature ($^{\circ}\text{C}$) measured at 10cm below the soil surface.

SurfTemp = Surface soil temperature ($^{\circ}\text{C}$).

Moist = Moisture measured on a scale from 0-10 where 0 is completely dry and 10 is saturated soil.

Glacier National Park Divide Mountain Undisturbed				
	Comp	SubTemp	SurfTemp	Moist
n	60	60	60	60
\bar{x}	1.69	14.92	32.06	-
M	1.67	15.00	31.65	8.00
s	0.39	2.75	5.18	-
Min	1.00	10.00	19.90	2.00
Max	2.83	20.00	43.00	10.00
Range	1.83	10.00	23.10	8.00

Gopher-disturbed				
	Comp	SubTemp	SurfTemp	Moist
n	60	60	60	60
\bar{x}	1.03	14.93	28.49	-
M	1.00	13.00	29.50	9.00
s	0.44	5.50	9.86	-
Min	0.25	6.00	7.90	0.00
Max	2.08	26.00	46.00	10.00
Range	1.83	20.00	38.10	10.00

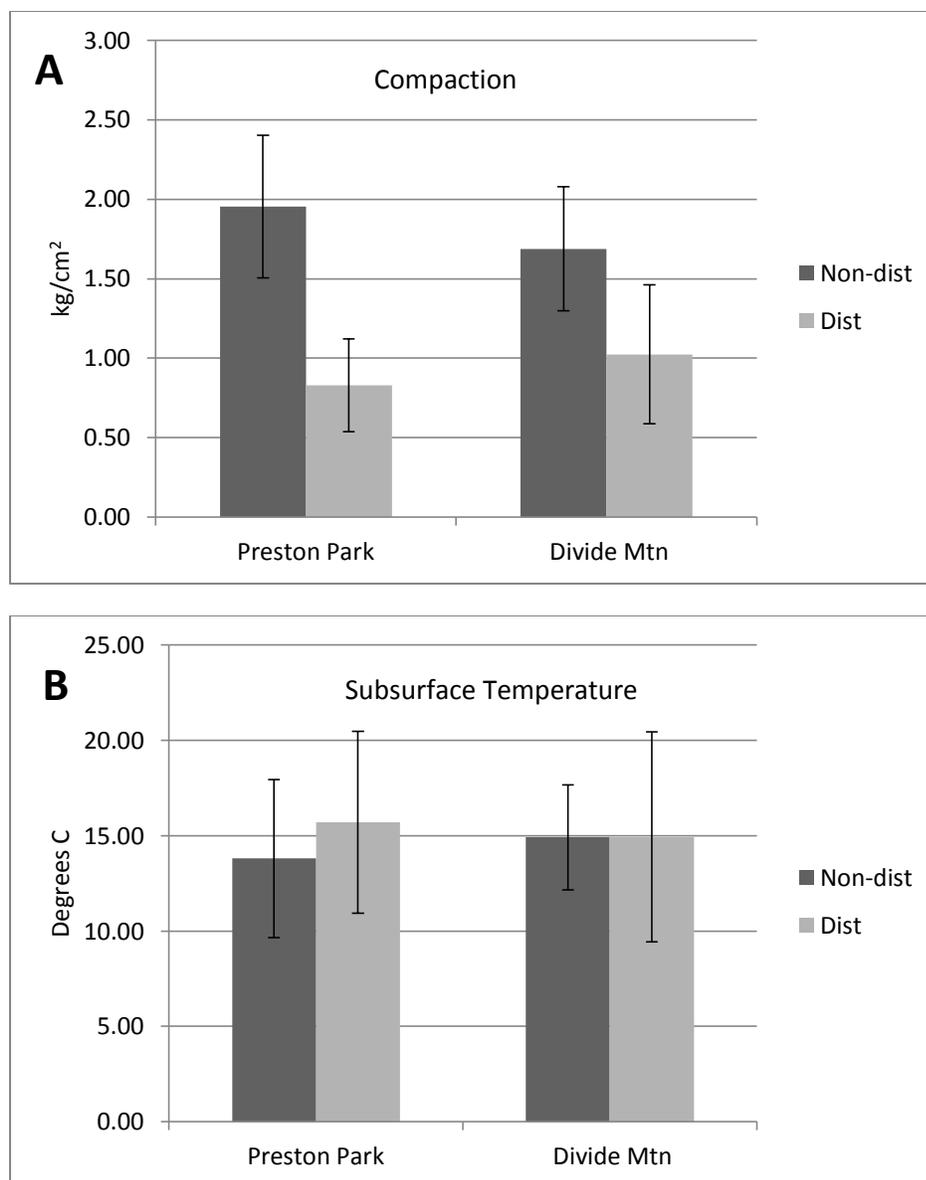


Figure 29. Results of soil compaction and subsurface soil temperature data at Preston Park and Divide Mountain, Glacier National Park, Montana. Dark grey bars represent undisturbed soils and light grey bars display gopher-disturbed soil data. Panel A shows the differences in soil compaction (kg/cm^2) between undisturbed and disturbed soils. Panel B displays subsurface soil temperatures ($^{\circ}\text{C}$) on undisturbed and disturbed soils. Error bars display one standard deviation above and below the mean.

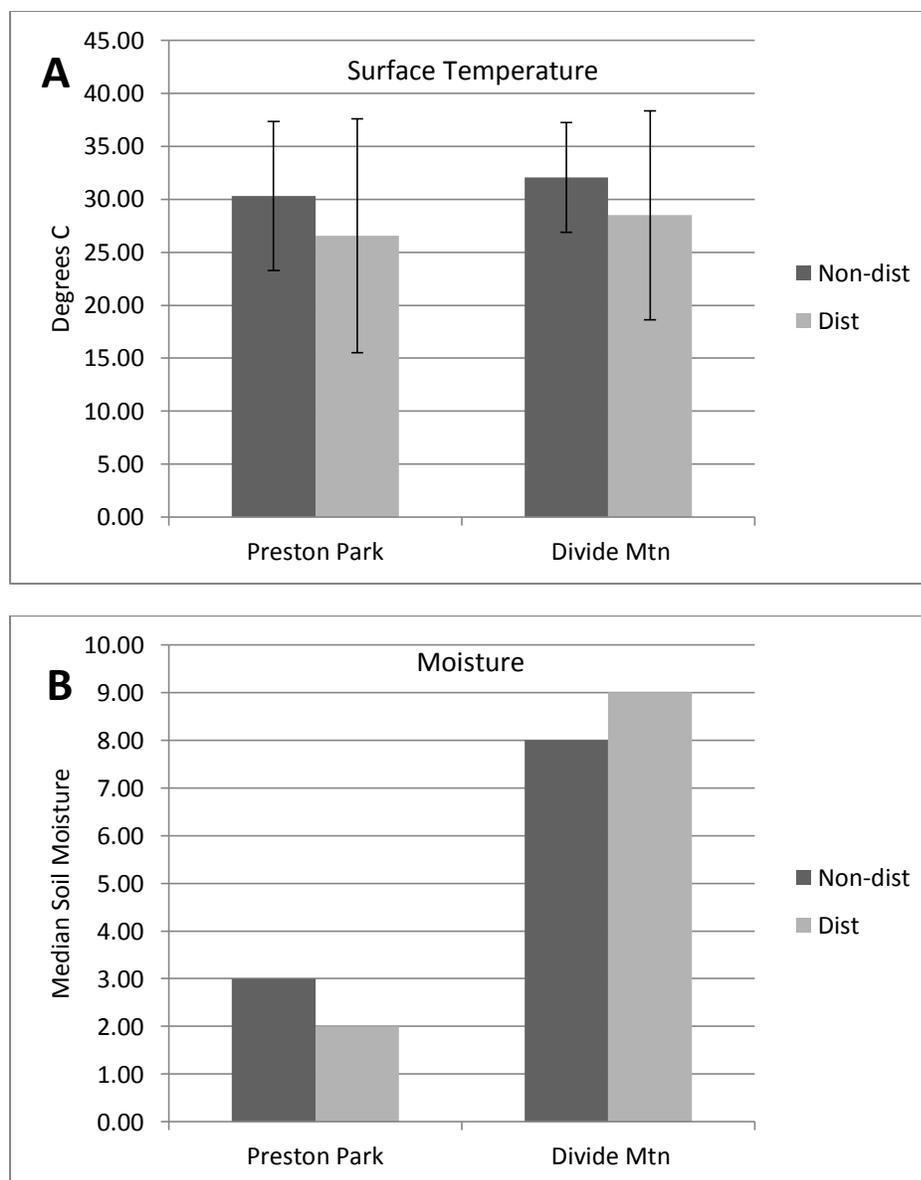


Figure 30. Results of soil surface temperature and soil moisture data at Preston Park and Divide Mountain, Glacier National Park, Montana. Dark grey bars represent undisturbed soils and light grey bars display gopher-disturbed soil data. Panel A exhibits soil surface temperatures ($^{\circ}\text{C}$) and panel B shows soil moisture measured on a scale from 0 to 10. Zero corresponds to dry soils and a value of 10 corresponds to saturated soils. Error bars display one standard deviation above and below the mean. No error bars were needed for ordinal data displayed in panel B.

Table 9. Correlation data between undisturbed soil characteristics as well as gopher-disturbed soil characteristics within Preston Park, Glacier National Park, Montana.

Comp = Soil compaction measured in kg/cm^2

SubTemp = Subsurface soil temperature ($^{\circ}\text{C}$) measured at 10cm below the soil surface.

SurfTemp = Surface soil temperature ($^{\circ}\text{C}$).

Moist = Moisture measured on a scale from 0-10 where 0 is completely dry and 10 is saturated soil.

Glacier National Park

Correlation Table

Preston Park (n = 90)

Undisturbed

	Comp	SubTemp	SurfTemp	Moist
Comp	-	0.17*	-0.11	-0.18*
SubTemp	0.17*	-	-0.08	0.23**
SurfTemp	-0.11	-0.08	-	0.10
Moist	-0.18*	0.23**	0.10	-

*Correlation is significant at the 0.05 level

**Correlation is significant at the 0.01 level

Gopher-disturbed

	Comp	SubTemp	SurfTemp	Moist
Comp	-	0.15	-0.02	0.15
SubTemp	0.15	-	0.32**	0.23**
SurfTemp	-0.02	0.32**	-	-0.19*
Moist	0.15	0.23**	-0.19*	-

*Correlation is significant at the 0.05 level

**Correlation is significant at the 0.01 level

Table 10. Correlation data between undisturbed soil characteristics as well as gopher-disturbed soil characteristics at Divide Mountain, Glacier National Park, Montana.

Comp = Soil compaction measured in kg/cm^2

SubTemp = Subsurface soil temperature ($^{\circ}\text{C}$) measured at 10cm below the soil surface.

SurfTemp = Surface soil temperature ($^{\circ}\text{C}$).

Moist = Moisture measured on a scale from 0-10 where 0 is completely dry and 10 is saturated soil.

Glacier National Park
Correlation Table
Divide Mountain (n = 60)
Undisturbed

	Comp	SubTemp	SurfTemp	Moist
Comp	-	0.14	-0.09	-0.05
SubTemp	0.14	-	0.16	-0.20*
SurfTemp	-0.09	0.16	-	-0.04
Moist	-0.05	-0.20*	-0.04	-

*Correlation is significant at the 0.05 level

**Correlation is significant at the 0.01 level

Gopher-disturbed

	Comp	SubTemp	SurfTemp	Moist
Comp	-	-0.09	-0.28**	-0.12
SubTemp	-0.09	-	0.59*	0.17
SurfTemp	-0.28**	0.59*	-	0.22*
Moist	-0.12	0.17	0.22*	-

*Correlation is significant at the 0.05 level

**Correlation is significant at the 0.01 level

At the local scale in ONP, soil characteristics from Olympic Marmot burrows were compared to soil characteristics from the surrounding, undisturbed matrix (Tables 11, 12, and 13). The Hurricane Ridge sample site consisted of many marmot burrows distributed across a mosaic of alpine meadows and alpine tundra environment within the alpine treeline ecotone. The vegetation of the intra-burrow matrix was comprised of yarrow, lupines, a few cow parsnip plants, and grasses. The conifers around the meadow environment were primarily mature subalpine fir with the occasional Douglas-fir. No seedlings were observed on marmot disturbances.

Sampling at Blue Mountain, ONP occurred in an environment representative of the upper threshold of the alpine treeline ecotone. The environment consisted of heather and tundra-type grasses with patches of subalpine fir occurring as tree islands and krummholz in the near distance. No evidence of seedlings existed on abandoned burrows.

Sampling at Obstruction Point occurred in a series of meadows dominated by avalanche lilies and surrounded by subalpine fir. Some lupines and grasses also existed in this environment. Many of the abandoned burrows identified by the NPS were located under late-lying snowfields and were unable to be sampled. One juvenile subalpine fir tree (< 30cm) was observed growing on an abandoned marmot burrow (Figure 31).

Table 11. Data comparing undisturbed soils to marmot-disturbed sites at Hurricane Ridge, Olympic National Park, Washington.

Comp = Soil compaction measured in kg/cm^2

SubTemp = Subsurface soil temperature ($^{\circ}\text{C}$) measured at 10cm below the soil surface.

SurfTemp = Surface soil temperature ($^{\circ}\text{C}$).

Moist = Moisture measured on a scale from 0-10 where 0 is completely dry and 10 is saturated soil.

Olympic National Park Hurricane Ridge Undisturbed				
	Comp	SubTemp	SurfTemp	Moist
n	30	30	30	30
\bar{x}	1.69	15.30	29.30	-
M	1.63	15.50	29.55	0.00
s	0.61	2.83	8.27	-
Min	0.67	10.00	13.60	0.00
Max	3.17	21.00	47.00	2.00
Range	2.50	11.00	33.40	2.00
Marmot-disturbed				
	Comp	SubTemp	SurfTemp	Moist
n	30	30	30	30
\bar{x}	0.34	14.07	28.23	-
M	0.29	13.50	26.25	0.00
s	0.12	3.85	10.40	-
Min	0.25	9.00	13.50	0.00
Max	0.58	21.00	45.40	2.00
Range	0.33	12.00	31.90	2.00

Table 12. Data comparing undisturbed soils to marmot-disturbed sites at Blue Mountain, Olympic National Park, Washington.

Comp = Soil compaction measured in kg/cm^2

SubTemp = Subsurface soil temperature ($^{\circ}\text{C}$) measured at 10cm below the soil surface.

SurfTemp = Surface soil temperature ($^{\circ}\text{C}$).

Moist = Moisture measured on a scale from 0-10 where 0 is completely dry and 10 is saturated soil.

Olympic National Park Blue Mountain Undisturbed				
	Comp	SubTemp	SurfTemp	Moist
n	20	20	20	20
\bar{x}	1.90	15.15	34.16	-
M	1.83	15.00	35.60	1.00
s	0.62	1.93	5.05	-
Min	1.00	11.00	16.30	0.00
Max	3.75	19.00	39.30	2.00
Range	2.75	8.00	23.00	2.00

Marmot-disturbed				
	Comp	SubTemp	SurfTemp	Moist
n	20	20	20	20
\bar{x}	0.34	14.45	44.31	-
M	0.33	14.00	43.90	0.00
s	0.10	1.36	3.76	-
Min	0.25	12.00	34.60	0.00
Max	0.58	17.00	49.80	1.00
Range	0.33	5.00	15.20	1.00

Table 13. Data comparing undisturbed soils to gopher-disturbed sites at Obstruction Point, Olympic National Park, Washington.

Comp = Soil compaction measured in kg/cm^2

SubTemp = Subsurface soil temperature ($^{\circ}\text{C}$) measured at 10cm below the soil surface

SurfTemp = Surface soil temperature ($^{\circ}\text{C}$)

Moist = Moisture measured on a scale from 0-10 where 0 is completely dry and 10 is saturated soil.

Olympic National Park Obstruction Point Undisturbed				
	Comp	SubTemp	SurfTemp	Moist
n	11	11	11	11
\bar{x}	2.58	12.00	25.45	-
M	2.58	12.00	24.50	0.00
s	0.51	2.00	4.32	-
Min	1.83	8.00	19.80	0.00
Max	3.42	15.00	34.30	1.00
Range	1.58	7.00	14.50	1.00
Marmot-disturbed				
	Comp	SubTemp	SurfTemp	Moist
n	11	11	11	11
\bar{x}	0.82	12.73	34.12	-
M	0.67	13.00	36.10	0.00
s	0.70	2.57	6.39	-
Min	0.25	9.00	19.90	0.00
Max	2.75	17.00	41.90	0.00
Range	2.50	8.00	22.00	0.00



Figure 31. Juvenile subalpine fir tree growing on an abandoned marmot burrow. The seedling is approximately 30 cm in height. Obstruction Point, Olympic National Park, Washington.

Across all three sampling sites, many characteristics were similar. At no site was there evidence of marmot herbivory on surrounding trees. Also, atmospheric conditions ranged from partly to mostly sunny and ambient air temperature ranged from 15-18°C. Undisturbed soils were significantly more compacted ($M = 1.63$) than marmot-disturbed soils ($M = 0.29$), $z = -4.78$, $p < 0.001$, $r = -0.62$ (Figure 32). The same was true at Blue Mountain and Obstruction Point, where undisturbed soils were significantly more compacted (Blue, $M = 1.83$; Obstruction, $M = 2.58$) than marmot-disturbed soils (Blue,

$M = 0.33$; Obstruction, $M = 0.67$; Blue, $z = -3.92$, $p < 0.05$, $r = -0.62$; Obstruction, $z = -2.85$, $p < 0.05$, $r = -0.61$).

Subsurface soil temperatures on undisturbed soils at Hurricane Ridge were significantly warmer ($M = 15.5^{\circ}\text{C}$) than marmot-disturbed soils ($M = 13.5^{\circ}\text{C}$), $z = -2.06$, $p < 0.05$, $r = -0.27$ (Figure 32). This trend did not continue at Blue Mountain or Obstruction Point, where no significant difference in subsurface soil temperature was observed (Blue, $z = -1.20$, $p > 0.05$, $r = -0.19$; Obstruction, $z = -1.14$, $p > 0.05$, $r = -0.24$). No significant difference existed between undisturbed and marmot-disturbed soil surface temperatures ($z = -0.22$, $p > 0.05$, $r = -0.03$) at Hurricane Ridge but significant differences existed at both Blue Mountain ($z = -3.85$, $p < 0.001$, $r = -0.61$) and Obstruction Point ($z = -2.76$, $p < 0.05$, $r = -0.59$; Figure 33). Soil surface temperatures were significantly cooler on undisturbed soils (Blue, $M = 35.6^{\circ}\text{C}$; Obstruction, $M = 24.5^{\circ}\text{C}$) than marmot-disturbed soils (Blue, $M = 43.9^{\circ}\text{C}$; Obstruction, $M = 36.1^{\circ}\text{C}$).

Soil moisture on undisturbed and marmot-disturbed soils at Hurricane Ridge were not different ($z = -1.36$, $p > 0.05$, $r = -0.17$; Figure 33). Nor were soil moisture values different at Obstruction Point ($z = -1.41$, $p > 0.05$, $r = -0.30$). Although Blue Mountain soils were exceedingly dry, soil moisture on undisturbed soils was significantly more moist ($M = 1$) than marmot-disturbed soils ($M = 0$), $z = -2.00$, $p < 0.05$, $r = -0.32$.

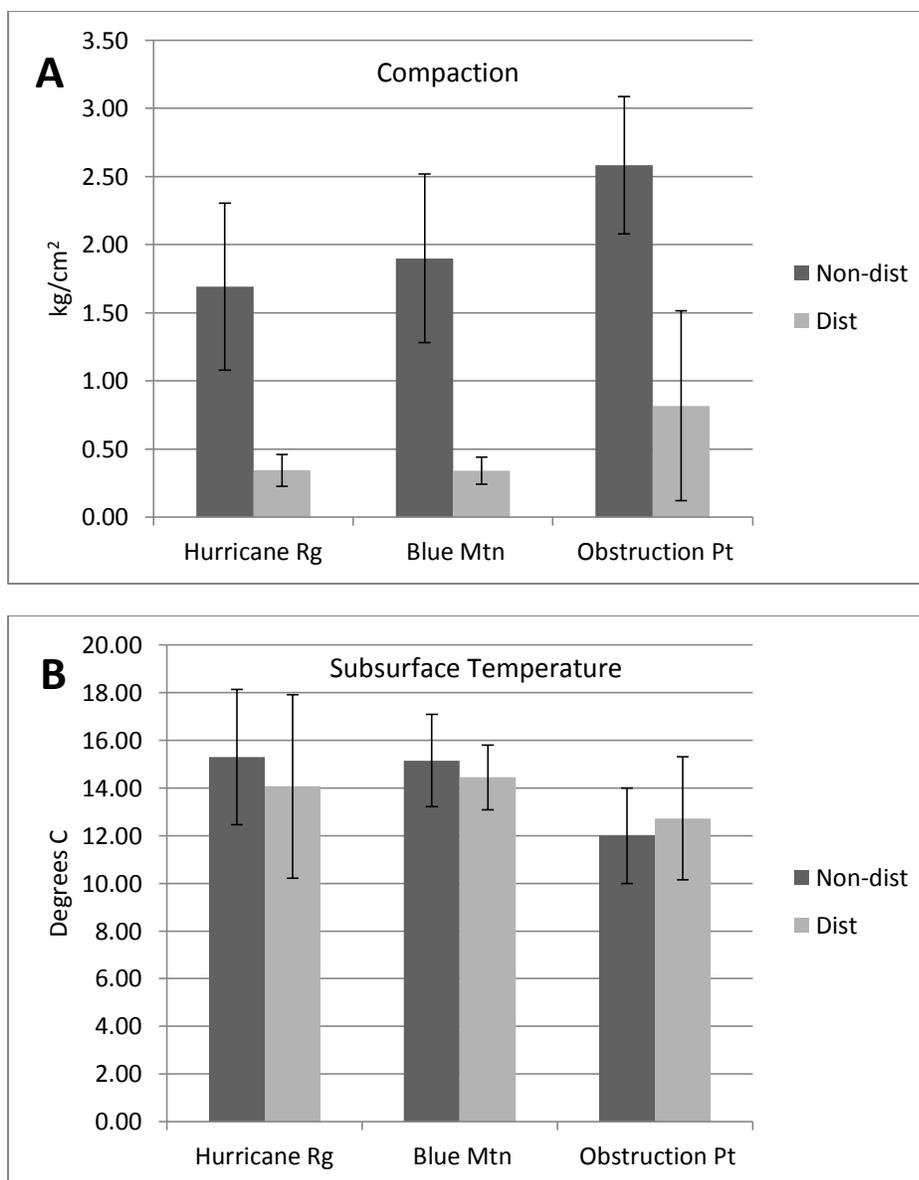


Figure 32. Results of soil compaction and subsurface soil temperature data at Hurricane Ridge, Blue Mountain, and Obstruction Point, Olympic National Park, Washington. Dark grey bars represent undisturbed soils and light grey bars display marmot-disturbed soil data. Panel A shows the differences in soil compaction (kg/cm²) between undisturbed and disturbed soils. Panel B displays subsurface soil temperatures (°C) on undisturbed and disturbed soils. Error bars display one standard deviation above and below the mean.

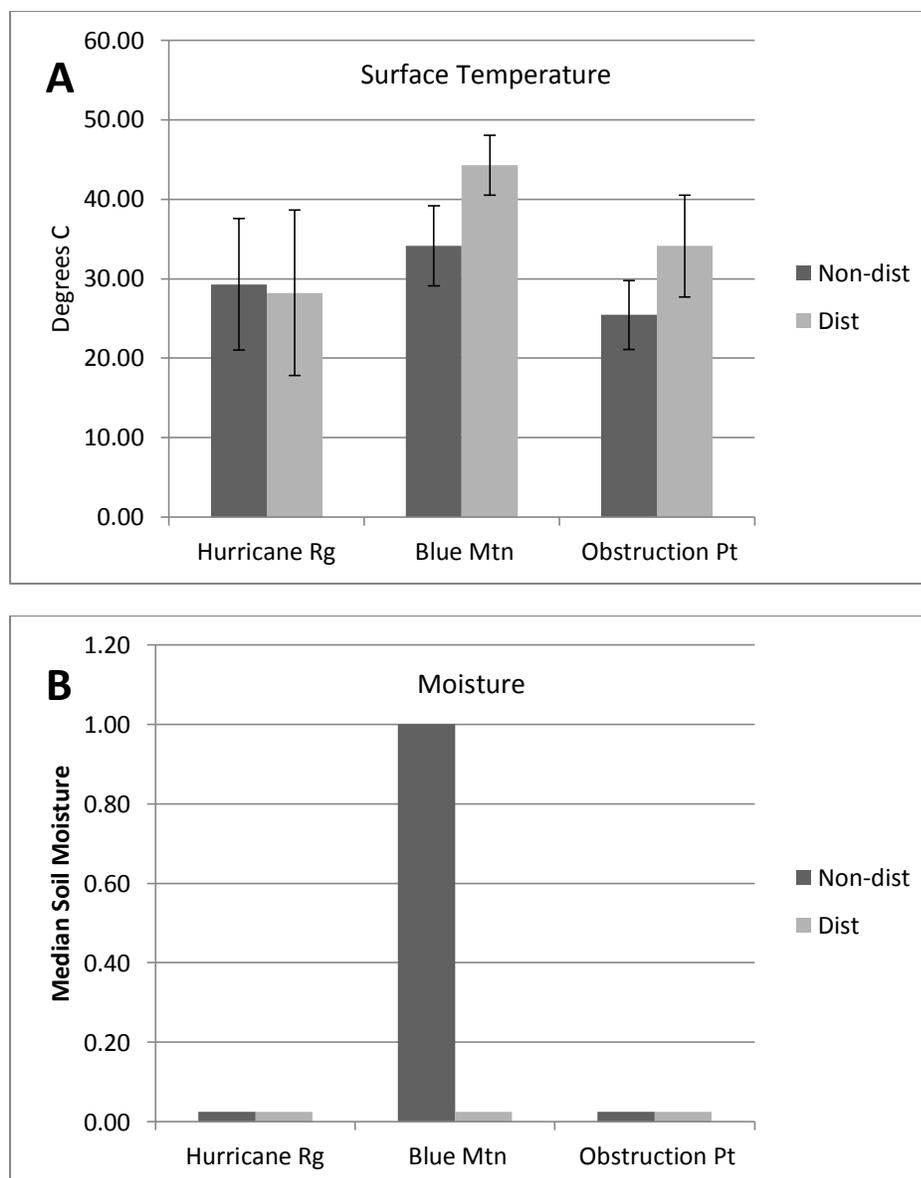


Figure 33. Results of soil surface temperature and soil moisture data at Hurricane Ridge, Blue Mountain, and Obstruction Point, Olympic National Park, Washington. Dark grey bars represent undisturbed soils and light grey bars display marmot-disturbed soil data. Panel A exhibits soil surface temperatures ($^{\circ}\text{C}$) and panel B shows soil moisture measured on a scale from 0 to 10. Zero corresponds to dry soils and a value of 10 corresponds to saturated soils. Error bars display one standard deviation above and below the mean. No error bars were needed for ordinal data displayed in panel B.

Similar to findings in GNP, many correlations existed between variables on undisturbed and marmot-disturbed soils at study sites in ONP. At Hurricane Ridge on undisturbed soils, correlations existed between surface temperature and soil compaction, and subsurface temperature. Moisture was also correlated with surface temperature (Table 14). On disturbed substrate, the only significant correlation occurred between surface and subsurface temperatures. At Blue Mountain, undisturbed soils revealed a correlation between surface and subsurface temperature, and disturbed areas showed a relationship between soil compaction and surface temperature (Table 15). Obstruction Point, similar to the rest, showed a relationship between surface and subsurface temperature on undisturbed soils as well as a correlation between moisture and surface temperature. Marmot-disturbed substrates revealed a correlation between surface and subsurface temperatures (Table 16).

Table 14. Correlation data between undisturbed soil characteristics as well as marmot-disturbed soil characteristics at Hurricane Ridge, Olympic National Park, Washington.
 Comp = Soil compaction measured in kg/cm^2
 SubTemp = Subsurface soil temperature ($^{\circ}\text{C}$) measured at 10cm below the soil surface.
 SurfTemp = Surface soil temperature ($^{\circ}\text{C}$).
 Moist = Moisture measured on a scale from 0-10 where 0 is completely dry and 10 is saturated soil.

Olympic National Park
 Correlation Table
 Hurricane Ridge (n = 30)
 Undisturbed

	Comp	SubTemp	SurfTemp	Moist
Comp	-	0.24	.356**	-0.08
SubTemp	0.24	-	.360**	-0.19
SurfTemp	.356**	.360**	-	-0.33**
Moist	-0.08	-0.19	0.10	-

**Correlation is significant at the 0.01 level

Marmot-disturbed

	Comp	SubTemp	SurfTemp	Moist
Comp	-	0.08	0.23	-0.06
SubTemp	0.08	-	.548**	-0.07
SurfTemp	0.23	.548**	-	0.10
Moist	-0.16	-0.21	-0.04	-

**Correlation is significant at the 0.01 level

Table 15. Correlation data between undisturbed soil characteristics as well as marmot-disturbed soil characteristics at Blue Mountain, Olympic National Park, Washington.

Comp = Soil compaction measured in kg/cm^2

SubTemp = Subsurface soil temperature ($^{\circ}\text{C}$) measured at 10cm below the soil surface.

SurfTemp = Surface soil temperature ($^{\circ}\text{C}$).

Moist = Moisture measured on a scale from 0-10 where 0 is completely dry and 10 is saturated soil.

Olympic National Park

Correlation Table

Blue Mountain (n = 20)

Undisturbed

	Comp	SubTemp	SurfTemp	Moist
Comp	-	0.14	-0.01	-0.34
SubTemp	0.14	-	-0.34*	0.07
SurfTemp	-0.01	-0.34*	-	0.19
Moist	-0.34	0.07	0.19	-

*Correlation is significant at the 0.05 level

Marmot-disturbed

	Comp	SubTemp	SurfTemp	Moist
Comp	-	0.06	0.46*	0.08
SubTemp	0.20	-	0.18	-0.19
SurfTemp	0.46*	0.18	-	-0.17
Moist	0.08	-0.19	-0.17	-

*Correlation is significant at the 0.05 level

Table 16. Correlation data between undisturbed soil characteristics as well as marmot-disturbed soil characteristics at Obstruction Point, Olympic National Park, Washington.

Comp = Soil compaction measured in kg/cm^2

SubTemp = Subsurface soil temperature ($^{\circ}\text{C}$) measured at 10cm below the soil surface.

SurfTemp = Surface soil temperature ($^{\circ}\text{C}$).

Moist = Moisture measured on a scale from 0-10 where 0 is completely dry and 10 is saturated soil.

Olympic National Park
Correlation Table
Obstruction Point (n = 11)
Undisturbed

	Comp	SubTemp	SurfTemp	Moist
Comp	-	-0.04	-0.19	-0.13
SubTemp	-0.04	-	-0.64**	-0.50
SurfTemp	-0.19	-0.64**	-	-0.58*
Moist	-0.13	-0.50	-0.58*	-

*Correlation is significant at the 0.05 level

**Correlation is significant at the 0.01 level

Marmot-disturbed

	Comp	SubTemp	SurfTemp	Moist
Comp	-	0.17	0.09	-
SubTemp	0.17	-	0.66**	-
SurfTemp	0.09	0.66**	-	-
Moist	-	-	-	-

*Correlation is significant at the 0.05 level

**Correlation is significant at the 0.01 level

Landscape Scale

Analysis at the landscape scale examines differences between undisturbed and disturbed soils within National Parks. In GNP, for example, the landscape scale assessed differences in soil characteristics between Preston Park and Divide Mountain. At this level of analysis, many statistical differences were apparent. A statistical difference existed in undisturbed soil compaction between Preston Park ($M = 1.92$) and Divide Mountain ($M = 1.67$; $U = 1773.5$, $z = -3.56$, $p < 0.001$, $r = -0.29$; (Tables 7 and 8, Figures 29 and 30). The same is true of gopher-disturbed soils between Preston Park ($M = 0.75$) and Divide Mountain ($M = 1.00$) ($U = 1989.5$, $z = -2.73$, $p < 0.05$, $r = -0.22$; Figure 21). In addition, a statistical difference exists in undisturbed subsurface soil temperatures between Preston Park ($M = 13^{\circ}\text{C}$) and Divide Mountain ($M = 15^{\circ}\text{C}$; $U = 1933.5$, $z = -2.96$, $p < 0.05$, $r = -0.24$), whereas, no difference existed between gopher-disturbed subsurface soil temperatures in Preston Park and Divide Mountain ($U = 2547$, $z = -0.59$, $p > 0.05$, $r = -0.05$). Surface soil temperatures revealed no difference in undisturbed soil temperatures ($U = 2320.5$, $z = -1.46$, $p > 0.05$, $r = -0.12$) nor gopher-disturbed soil temperatures ($U = 2440.5$, $z = -0.99$, $p > 0.05$, $r = -0.08$) between Preston Park and Divide Mountain. A significant difference existed in both undisturbed soil moisture ($U = 629.5$, $z = -7.99$, $p < 0.001$, $r = -0.65$) and gopher-disturbed soil moisture ($U = 170$, $z = -9.91$, $p < 0.001$, $r = -0.81$) between Preston Park and Divide Mountain.

Comparisons between Hurricane Ridge, Blue Mountain, and Obstruction Point in ONP revealed a significant difference in soil compaction of undisturbed soils between the three study sites of ONP ($X^2(2) = 15.04$, $p < 0.05$; Figure 31). Posthoc Wilcoxon tests and a Bonferroni correction demonstrated that soil compaction did not differ

significantly between Hurricane Ridge and Blue Mountain ($T = 573.5$, $r = -0.18$) but was significantly different between Hurricane Ridge and Obstruction Point ($T = 353.5$, $r = -0.56$) as well as between Obstruction Point and Blue Mountain ($T = 244.5$, $r = -0.56$). Marmot-disturbed soils also revealed a significant difference in soil compaction between sites of ONP ($X^2(2) = 12.90$, $p < 0.05$). Soil compaction did not differ significantly between Hurricane Ridge and Blue Mountain ($T = 525.5$, $z = -0.33$, $r = -0.05$) but was significantly different between Hurricane Ridge and Obstruction Point ($T = 342.5$, $z = -3.39$, $r = -0.53$) as well as between Obstruction Point and Blue Mountain ($T = 247.5$, $z = -3.07$, $r = -0.55$).

In addition to differences in soil compaction, a significant difference was present in subsurface soil temperatures of undisturbed soils between sites of ONP ($X^2(2) = 13.28$, $p < 0.05$). Subsurface soil temperature did not differ significantly between Hurricane Ridge and Blue Mountain ($T = 496$, $z = -0.28$, $r = -0.04$), but was significantly different between Hurricane Ridge and Obstruction Point ($T = 121.5$, $z = -3.24$, $r = -0.51$) as well as between Obstruction Point and Blue Mountain ($T = 93$, $z = -3.46$, $r = -0.62$). Unlike soil compaction, however, differences in subsurface soil temperatures were confined to undisturbed soils and no difference in subsurface soil temperature existed on marmot-disturbed soils between ONP study sites ($X^2(2) = 3.08$, $p > 0.05$).

Surface soil temperatures of undisturbed soils between ONP sites were also significant ($X^2(2) = 12.90$, $p < 0.05$). No difference existed between Hurricane Ridge and Blue Mountain ($T = 626.5$, $z = -2.31$, $r = -0.33$), nor was surface temperature significantly different between Hurricane Ridge and Obstruction Point ($T = 181$, $z = -1.47$, $r = -0.23$), but a significant difference was present between Obstruction Point and

Blue Mountain ($T = 86$, $z = -3.72$, $r = -0.67$). Surface soil temperature of marmot-disturbed soils between sites of ONP revealed significant differences ($X^2(2) = 29.72$, $p < 0.001$). Soil surface temperatures were significantly different between Hurricane Ridge and Blue Mountain ($T = 516.5$, $z = -4.92$, $r = -0.70$), but not significant between Hurricane Ridge and Obstruction Point ($T = 289$, $z = -1.71$, $r = -0.27$). Soil surface temperatures were also different between Obstruction Point and Blue Mountain ($T = 76$, $z = -4.13$, $r = -0.74$).

Significant variation in soil moisture of undisturbed soils existed between study sites of ONP ($X^2(2) = 10.35$, $p < 0.05$). Soil moisture was different between Hurricane Ridge and Blue Mountain ($T = 632$, $z = -2.81$, $r = -0.40$), but no differences were present between Hurricane Ridge and Obstruction Point ($T = 221.5$, $z = -0.39$, $r = -0.06$) nor between Obstruction Point and Blue Mountain ($T = 123.5$, $z = -2.47$, $r = -0.44$). Similar findings between marmot-disturbed soils of ONP highlighted significant differences in soil moisture ($X^2(2) = 6.22$, $p < 0.05$). Soil moisture was not significantly different between Hurricane Ridge and Blue Mountain ($T = 474$, $z = -0.85$, $r = -0.12$), between Hurricane Ridge and Obstruction Point ($T = 165$, $z = -2.44$, $r = -0.38$), nor between Obstruction Point and Blue Mountain ($T = 143$, $z = -1.99$, $r = -0.36$).

Regional Scale

The regional scale was used to assess differences in soil characteristics between GNP and ONP. Analysis at the regional scale evaluates the impact of gophers in GNP and marmots in ONP on soil characteristics and potential effect on conifer germination

and survival. Results of the regional scale soil characteristics are summarized in Tables 17 and 18.

Comparing soil compaction between GNP and ONP, no difference exists between undisturbed soils ($U = 4418.5$, $z = -0.39$, $p > 0.05$, $r = -0.03$; Figure 34). Undisturbed soils appear to have relatively equal soil compaction rates independent of national park. Disturbed soils, however, reveal a significant difference in disturbed soil compaction between GNP and ONP ($U = 913$, $z = -9.14$, $p < 0.001$, $r = -0.63$). Gopher-disturbed soils are significantly more compacted ($M = 0.83$) than marmot-disturbed soils ($M = 0.33$).

Undisturbed soils had similar subsurface soil temperatures ($U = 3938.5$, $z = -1.59$, $p > 0.05$, $r = -0.11$; Figure 34) between national parks but a slightly significant difference ($U = 3772$, $z = -2.00$, $p < 0.05$, $r = -0.14$) existed between subsurface soil temperatures on disturbed soils between parks, with gopher-disturbed soils being slightly warmer ($M = 16^{\circ}\text{C}$) than marmot-disturbed soils ($M = 14^{\circ}\text{C}$). Furthermore, soil surface temperatures on undisturbed soils are comparable between parks ($U = 4332$, $z = -0.60$, $p > 0.05$, $r = -0.04$), whereas, surface temperatures on disturbed soils are significantly different ($U = 2829.5$, $z = -4.342$, $p < 0.001$, $r = -0.30$). Surface temperatures were cooler on gopher-disturbed soils ($M = 26.8^{\circ}\text{C}$) and warmer on marmot-disturbed soils ($M = 36.8^{\circ}\text{C}$; Figure 35).

At the regional scale, the only variable that was significantly different between parks on both undisturbed and disturbed soils was soil moisture. Undisturbed soils in GNP were significantly more moist ($M = 6$) than undisturbed soils in ONP ($M = 0$), $U = 454.5$, $z = -10.35$, $p < 0.001$, $r = -0.71$. Similar findings on mammal-disturbed soils

indicated that soil moisture on undisturbed soils in GNP were more moist ($M = 3$) than disturbed soils in ONP ($M = 0$), $U = 276.5$, $z = -10.85$, $p < 0.001$, $r = -0.75$; Figure 35).

Table 17. Data comparing undisturbed soils in Glacier National Park, Montana, to undisturbed soils in Olympic National Park, Washington.

Comp = Soil compaction measured in kg/cm^2

SubTemp = Subsurface soil temperature ($^{\circ}\text{C}$) measured at 10cm below the soil surface.

SurfTemp = Surface soil temperature ($^{\circ}\text{C}$).

Moist = Moisture measured on a scale from 0-10 where 0 is completely dry and 10 is saturated soil.

Glacier National Park Undisturbed				
	Comp	SubTemp	SurfTemp	Moist
n	150	150	150	150
\bar{x}	1.85	14.25	31.01	-
M	1.83	14.00	31.30	6.00
s	0.44	3.67	6.41	-
Min	1.00	8.00	13.30	0.00
Max	3.50	28.00	45.50	10.00
Range	2.50	20.00	32.20	10.00

Olympic National Park Undisturbed				
	Comp	SubTemp	SurfTemp	Moist
n	61	61	61	61
\bar{x}	1.92	14.66	30.20	-
M	1.83	15.00	31.30	0.00
s	0.67	2.70	7.35	-
Min	0.67	8.00	13.60	0.00
Max	3.75	21.00	47.00	2.00
Range	3.08	13.00	33.40	2.00

Table 18. Data comparing fossorial mammal-disturbed soils in Glacier National Park, Montana, to fossorial mammal-disturbed soils in Olympic National Park, Washington.
 Comp = Soil compaction measured in kg/cm^2
 SubTemp = Subsurface soil temperature ($^{\circ}\text{C}$) measured at 10cm below the soil surface.
 SurfTemp = Surface soil temperature ($^{\circ}\text{C}$).
 Moist = Moisture measured on a scale from 0-10 where 0 is completely dry and 10 is saturated soil.

Glacier National Park Disturbed				
	Comp	SubTemp	SurfTemp	Moist
n	150	150	150	150
\bar{x}	0.91	15.40	27.33	-
M	0.83	16.00	26.80	3.00
s	0.37	5.07	10.58	-
Min	0.25	6.00	7.90	0.00
Max	2.08	27.00	47.60	10.00
Range	1.83	21.00	39.70	10.00

Olympic National Park Disturbed				
	Comp	SubTemp	SurfTemp	Moist
n	61	61	61	61
\bar{x}	0.43	13.95	34.56	-
M	0.33	14.00	36.80	0.00
s	0.35	3.04	10.74	-
Min	0.25	9.00	13.50	0.00
Max	2.75	21.00	49.80	2.00
Range	2.50	12.00	36.30	2.00

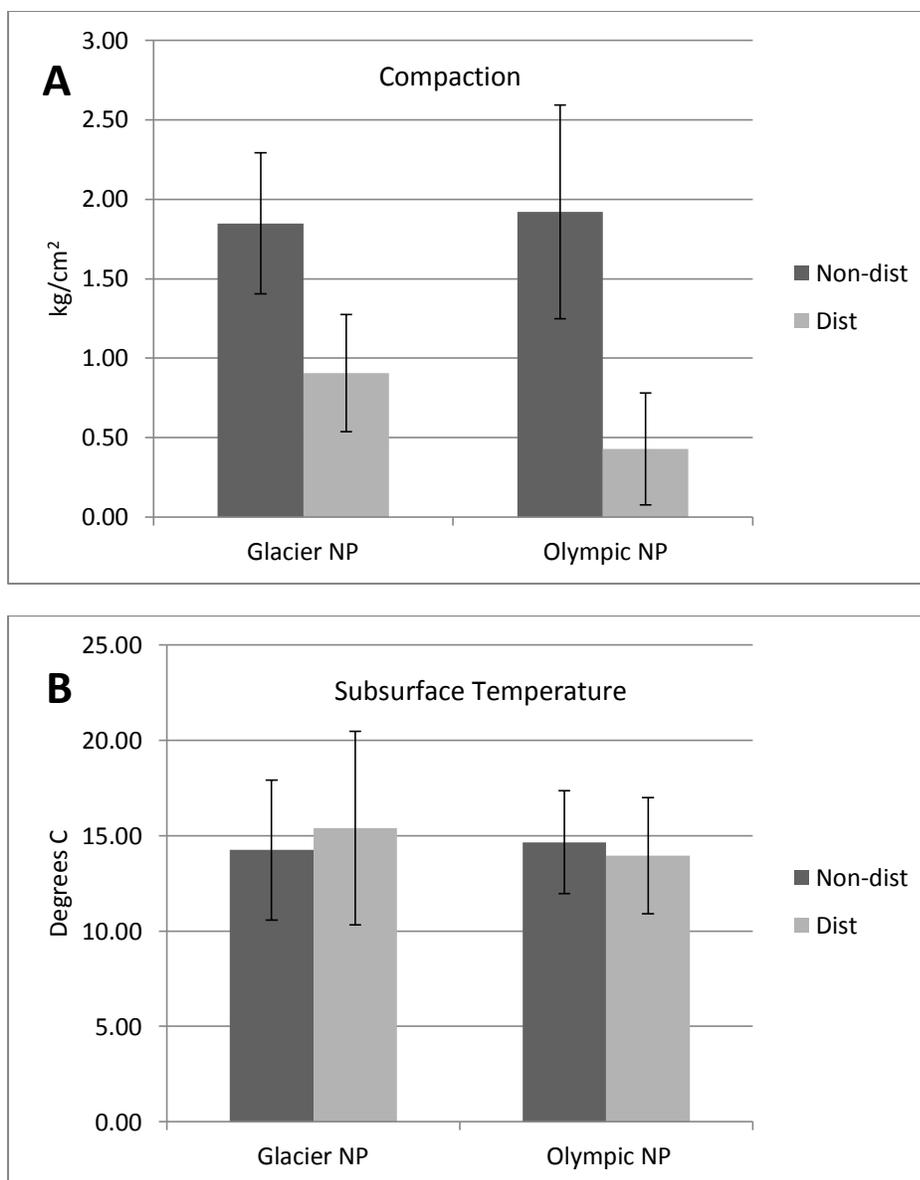


Figure 34. Soil compaction and subsurface soil temperature data at Glacier National Park, Montana, and Olympic National Park, Washington. Dark grey bars represent undisturbed soils and light grey bars display mammal-disturbed soil data. Panel A shows the differences in soil compaction (kg/cm²) between undisturbed and disturbed soils. Panel B displays subsurface soil temperatures (°C) on undisturbed and disturbed soils. Error bars display one standard deviation above and below the mean.

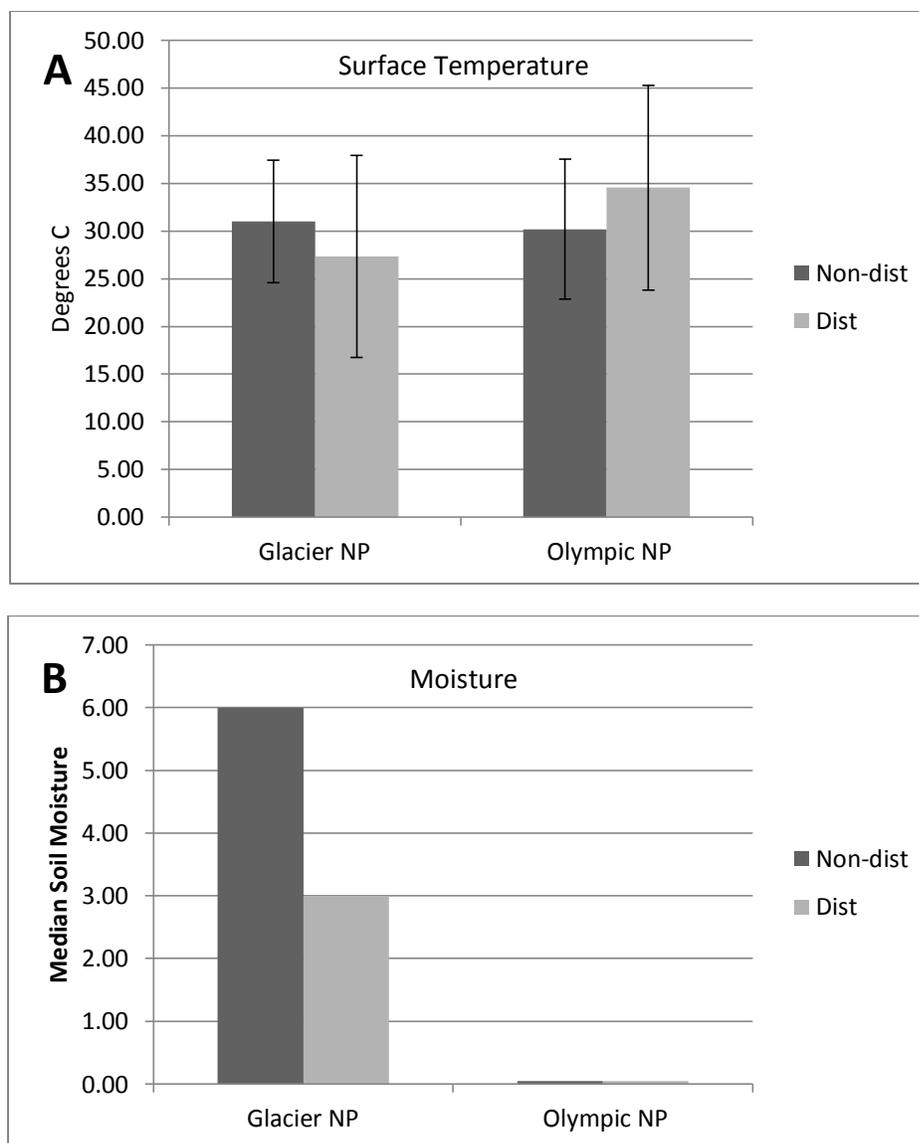


Figure 35. Soil surface temperature and soil moisture data at Glacier National Park, Montana, and Olympic National Park, Washington. Dark grey bars represent undisturbed soils and light grey bars display marmot-disturbed soil data. Panel A exhibits soil surface temperatures ($^{\circ}\text{C}$) and panel B shows soil moisture measured on a scale from 0 to 10. Zero corresponds to dry soils and a value of 10 corresponds to saturated soils. Error bars display one standard deviation above and below the mean. No error bars were needed for ordinal data displayed in panel B.

Laboratory Analysis

The results from the soil analyses revealed that soil textures within parks and between parks were exceedingly similar (Table 19). In GNP, undisturbed soils at Preston Park and Divide Mountain were loams and disturbed soils were loam at Preston Park and clay loam at Divide. In ONP, all soils, whether undisturbed or disturbed, were loam. The greenhouse control soil was a sandy loam.

Soil pH among samples ranged from 4.6 at Blue Mountain in ONP to 6.8 at Divide Mountain in GNP. No consistent pattern existed between undisturbed and disturbed pH values. Disturbed soils in Preston Park were more acidic (4.8) than undisturbed soils (5.0) and a similar trend was apparent in ONP, where an increase in acidity occurred on disturbed soils at Hurricane Ridge and Blue Mountain. Divide Mountain in GNP, however, experienced an increase in alkalinity on disturbed soils compared to undisturbed, and Obstruction Point soils in ONP had identical soil pH independent of soil disturbance or lack thereof. The greenhouse soil had a pH of 7.8.

Salinity ranged from 0.2 decisiemens per meter (dS/m) at Obstruction Point, ONP to 0.7 dS/m at Divide Mountain, GNP, and was highly variable among samples. In some locations (Preston Park, GNP, and Obstruction Point, ONP), salinity was equal between undisturbed and disturbed soils. At other sites (Divide Mountain, GNP, and Hurricane Ridge, ONP), salinity was higher in disturbed soils, whereas at Blue Mountain, ONP, salinity decreased in disturbed soils. Salinity of the greenhouse control soil was 0.5 dS/m.

The availability of macronutrients was also highly variable between samples. P, similar to salinity, increased in disturbed soils at some locations (Preston Park, GNP,

Blue Mountain, ONP, and Obstruction Point, ONP) when compared to undisturbed and decreased at other sites (Divide Mountain, GNP, and Hurricane Ridge, ONP). P ranged from 5.8 mg/kg in disturbed soils at Divide Mountain, GNP, to 96 mg/kg in disturbed soils at Obstruction Point, ONP. K was more consistent than P with a reduction in K occurring at most disturbed sites, when compared to undisturbed, with the exception of Blue Mountain, ONP. Potassium values, however, revealed a much larger range of potassium levels. K ranged from 116 mg/kg on disturbed soils at Divide Mountain, GNP, to 247 mg/kg on disturbed soils at Blue Mountain, ONP. Preston Park, GNP, contained nearly twice the K of Divide Mountain, GNP, and both Hurricane Ridge and Blue Mountain, ONP, contained substantially more K than Obstruction Point, ONP. Greenhouse soils had a K of 391 mg/kg.

The only soil test in which a consistent pattern was observed was percent organic matter. At all study sites within parks and between parks, disturbed soils contained less organic matter than undisturbed soils. Organic matter on undisturbed soils ranged from 8.6% at Divide Mountain, GNP, to 15.6% at Obstruction Point, ONP. Disturbed soils had an organic matter range of 6.5% at Divide Mountain, GNP, to 12.6% at Preston Park, GNP. The greenhouse control soil contained 3.3% organic matter.

Table 19. Results from laboratory soil analysis. Note the relative uniformity of soil characteristics between sites.

ND = undisturbed soils

D = disturbed soils

Tex = soil texture (L = loam, CL = clay loam, SL = sandy loam)

Sal = salinity measured in dS/m

P = phosphorous measured in mg/kg

K = potassium measured in mg/kg

OM = percent organic matter

Variable	Glacier National Park				Olympic National Park						
	Preston P.		Divide Mtn.		Hurr. Rg.		Blue Mtn.		Obst. Pt.		Contr
	ND	D	ND	D	ND	D	ND	D	ND	D	Contr
Tex	L	L	L	CL	L	L	L	L	L	L	SL
pH	5	4.8	6.2	6.8	4.9	4.6	5.8	5.6	5.2	5.2	7.8
Sal	0.3	0.3	0.5	0.7	0.3	0.4	0.3	0.2	0.2	0.2	0.5
P	28	31.9	6.2	5.8	28	17.7	22	27	34	96	88
K	212	211	121	116	204	162	206	247	150	133	391
OM	13.2	12.6	8.6	6.5	11.4	9.6	10.3	7.8	15.6	7.8	3.3

Germination Experiment

Experimental seed germination was conducted at the same scales as the soil characteristics mentioned above. Subalpine fir germination experiments were conducted at the local scale, aggregated to the landscape scale, and lastly, aggregated to the regional scale. Germination in control soils was also conducted to allow for the assessment of soil compaction on seed germination. The results of the germination tests are shown in tables 20 – 24.

At the local scale, there was no statistical difference in subalpine fir germination between undisturbed and disturbed soils at Preston Park ($X^2(1) = 0.14, p > 0.05$) or Divide Mountain ($X^2(1) = 1.68, p > 0.05$; Table 20). It is interesting to note, however, that although no statistical differences existed between germination rates on undisturbed and disturbed soils at either GNP site, overall germination at Divide Mountain was more than double that of soils at Preston Park (Table 20). In ONP, no statistical difference existed between germination on undisturbed and disturbed soils at Hurricane Ridge ($X^2(1) = 0.06, p > 0.05$), and Obstruction Point ($X^2(1) = 0, p > 0.05$; Table 21). There was a statistically significant difference, however, at Blue Mountain, where more seeds remained viable and germinated in disturbed soils ($N = 11$) than in undisturbed soils ($N = 3, X^2(1) = 8.57, p < 0.05$; Table 21). At the landscape scale within GNP, undisturbed and disturbed soils did not reveal a significant effect on seed germination ($X^2(1) = 2.50, p > 0.05$; Table 22), whereas, within ONP, seed germination on disturbed soils was nearly double ($N = 29$) that of germination on undisturbed ($N = 16, X^2(1) = 8.19, p < 0.05$; Table 22). At the regional scale, germination was significantly higher on disturbed soils ($N = 48$) than on undisturbed soils ($N = 31, X^2(1) = 8.29, p < 0.05$; Table 24).

Within the control soils, there was no significant difference in germination on undisturbed or disturbed soils of GNP ($X^2(1) = 0.68, p > 0.05$) nor ONP ($X^2(1) = 1.43, p > 0.05$). Although many of the differences in germination on undisturbed and disturbed soils were non-significant, it is important to note that higher rates of germination occurred on disturbed soils at all study sites and across all scales.

Table 20. Local scale germination results in Glacier National Park, Montana.

ND = Undisturbed soils, D = Disturbed soils

NG = No germination, G = Germination

	Local Scale Glacier NP Preston Park	
	NG	G
	<hr/>	
ND (n = 15)	10 (67%)	5 (33%)
D (n = 15)	9 (60%)	6 (40%)

	Divide Mountain	
	NG	G
	<hr/>	
ND (n = 15)	5 (33%)	10 (67%)
D (n = 15)	2 (13%)	13 (87%)

Table 21. Local scale germination results in Olympic National Park, Washington.

ND = Undisturbed soils, D = Disturbed soils

NG = No germination, G = Germination

	Local Scale Olympic NP Hurricane Ridge	
	NG	G
	<hr/>	
ND (n = 15)	6 (40%)	9 (60%)
D (n = 14)	5 (36%)	9 (64%)

	Blue Mountain	
	NG	G
	<hr/>	
ND (n = 15)	12 (80%)	3 (20%)
D (n = 15)	4 (27%)	11 (73%)

	Obstruction Point	
	NG	G
	<hr/>	
ND (n = 15)	11 (73%)	4 (27%)
D (n = 15)	6 (40%)	9 (60%)

Table 22. Landscape scale germination results in Glacier and Olympic National Parks.

ND = Undisturbed soils, D = Disturbed soils

NG = No germination, G = Germination

	Landscape Scale Glacier NP	
	NG	G
ND (n = 30)	15 (50%)	15 (50%)
D (n = 30)	9 (30%)	21 (70%)

	Olympic NP	
	NG	G
ND (n = 45)	29 (64%)	16 (36%)
D (n = 44)	15 (34%)	29 (66%)

Table 23. Control soil germination results for soil compaction observed in Glacier and Olympic National Parks.

ND = Undisturbed soils, D = Disturbed soils

NG = No germination, G = Germination

	Control Soil Glacier NP	
	NG	G
ND (n = 15)	5 (33%)	10 (67%)
D (n = 15)	3 (20%)	12 (80%)

	Control Soil Olympic NP	
	NG	G
ND (n = 15)	6 (40%)	9 (60%)
D (n = 15)	3 (20%)	12 (80%)

Table 24. Regional scale results for seed germination in undisturbed and disturbed soils.

ND = Undisturbed soils, D = Disturbed soils

NG = No germination, G = Germination

	Regional Scale	
	NG	G
ND (n = 75)	44 (59%)	31 (41%)
D (n = 74)	26 (35%)	48 (65%)

CHAPTER 6

DISCUSSION AND CONCLUSIONS

Hypothesis 1 - The Sub-local Scale

The null hypothesis (H_0) for the sub-local scale is that physical soil characteristics (compaction rates, surface and subsurface temperatures, and soil texture) are the same for all undisturbed sites within a study area. Additionally, mammal-disturbed locations within each study area are also expected to be similar.

As was noted above, undisturbed sites within Preston Park had homogeneous soil compaction and surface temperature values. This result is not unexpected given the proximity of sampling sites within the hanging valley (approx. 200 m distance between sites), the consistency of vegetation, and the lack of perceptible environmental gradients in an area with an altitudinal range extending from 2128 m to 2189 m. Despite the homogeneous nature of Preston Park's physical soil characteristics, soil moisture and subsurface soil temperature varied among sampling locations. Although every effort was made to select undisturbed sites that were similar in physical soil characteristics, soil moisture was significantly different between site B and C as well as between site A and B. These differences are likely attributable to the several small streams that occupy Preston Park. All sample sites were limited to distances greater than 100 m from streams, but a small tarn and substantial snowpack exist near the headwall of the hanging valley, and subsurface flow is likely to be extensive and variable. Site B contained a slight slope

with a limited number of western false hellebore (*Veratrum californicttm* Durand), known to occupy moist soils in mountain environments (Whitson et al. 2006), plants at the toe of the slope. Soil moisture readings were slightly higher at the base of the slope and may have contributed to the difference in soil moisture between sampling locations. Soil moisture and subsurface soil temperatures were positively correlated, which is logical considering that variation in soil moisture has been shown to have an effect on soil temperatures (Al-Kayssi et al. 1990). Similar variation in soil moisture and temperature over relatively small areas has also been observed within the taiga-tundra ecotone in Northwestern Alaska (Stottlemeyer et al. 2001).

Gopher-disturbed soils within Preston Park exhibited similar variations in soil moisture and subsurface temperature between sampling locations, which are likely caused by the variability in soil moisture mentioned previously. Soil compaction and surface soil temperatures were also significantly different between disturbed sites within Preston Park. It has been noted in previous research that soil compaction of gopher eskers and mounds are less compact than soil in neighboring undisturbed areas (Sherrod and Seastedt 2001; Butler and Butler 2009). Furthermore, it has been suggested that gopher eskers erode within several weeks following exposure (Butler and Butler 2009; Knight 2009), but no data exist to validate these claims. Gopher mounds have been shown to persist for several years despite existing within an environment of active erosion (Sherrod and Seastedt 2001), and gopher eskers may exhibit similar permanence. It is likely, therefore, that soil compaction between sampling sites within Preston Park was significantly different because of various stages of decay on eskers. An esker that has been exposed for several weeks, or months, is likely to be more compacted, as soils

have settled and been rained upon, than soils that have recently been exposed by melting snowpack. The dates of exposure are not known for the gopher-disturbed sample sites, and it is unrealistic to assume that all eskers were exposed on the same date. Therefore, the differences observed in soil compaction between gopher-disturbed sites within Preston Park are likely the result of variation associated with esker exposure.

Differences in surface temperature on gopher-disturbed soils within Preston Park are possibly caused by differences in vegetation quantity and density growing adjacent to, and on, the surface of gopher eskers (Figure 36). The effects of vegetation on soil surface temperature has long been noted and incorporated into predictive models (Deardorff 1978). It is therefore likely that variations in soil surface temperatures on gopher eskers are the result of surrounding vegetation. It is interesting to note that a slight negative correlation existed between soil surface temperatures and soil moisture on gopher-disturbed soils. Despite the moderating effects of vegetative cover on gopher eskers, increased surface temperatures corresponded to decreased soil moisture. This is logical considering that gopher eskers are relatively non-compacted and an increase in insolation would result in increased evaporation. A strong positive correlation between summer soil surface and subsurface temperatures further validates this assumption where warmer surface temperatures are associated with warmer subsurface temperatures.

Sampling sites at Divide Mountain revealed some similarities and some differences between sampling locations. Similar to Preston Park, undisturbed soils at Divide Mountain were comparable in both soil compaction and surface temperatures between sites. Subsurface soil temperature between sites, however, was different, as it was in Preston Park, and is likely attributed to soil moisture as mentioned above. Soil

moisture, however, was not significantly different between Divide Mountain sample sites as it had been at Preston Park. During field campaigns in the months of July in both 2010 and 2011, localized afternoon thunderstorms, typical of summer months in mountain environments, occurred on some sampling sites. In 2010, sampling occurred 48 hours after a precipitation event at Divide Mountain. The precipitation equally saturated undisturbed soils and resulted in similar soil moisture readings between undisturbed sites. On gopher-disturbed soils at Divide Mountain, soil moisture was different between disturbed sites.

Soil compaction on gopher-disturbed soils at Divide Mountain was similar. Unlike Preston Park, which consists of subalpine meadows typically found at the lower extent of the alpine ecotone, Divide Mountain is more representative of the upper extent of the alpine ecotone where tree islands give way to alpine tundra. The more exposed environment, and lack of erect trees, may result in more uniform exposure of eskers and therefore, eskers that have eroded or degraded at similar rates and result in similar compaction. The more exposed nature of Divide Mountain also explains the negative correlation between soil compaction and soil surface temperatures. Less compacted soils were related to warmer surface temperatures which may be caused by increased pore space near the soil surface.



Figure 36. A gopher esker in Preston Park, Glacier National Park, Montana. Notice the abundance of vegetation growing around and on the esker.

Hypothesis 2 - The Local Scale

Hypothesis 2 (H₀2) assessed the differences in physical soil characteristics (compaction rates, surface and subsurface temperatures, and soil texture) at the same sample site and proposed that the factors were the same in both areas of mammal disturbance and undisturbed areas.

Glacier National Park

Comparing undisturbed to gopher-disturbed sites within Preston Park and Divide Mountain, similar trends develop between locations. Soil compaction was significantly less compact on gopher-disturbed soils than on undisturbed soils. These findings were consistent with previous research mentioned above. Surface temperatures were different between undisturbed and disturbed soils at each location. Based on literature associated with tilling of agricultural land, less compacted soil (tilled soil) contained greater surface area which was said to possibly increase soil temperature (Licht and Al-Kaisi 2005). Less compact soils contained greater pore space, which was believed to accommodate more soil air and moisture and influence soil temperature (Licht and Al-Kaisi 2005). In a Mediterranean environment in the coastal mountains of northern California, gopher mounds were significantly warmer than undisturbed soils (Eviner and Chapin 2005). Similar findings occurred within a low elevation grassland-oak savannah environment, where soil surface temperatures on gopher mounds were substantially warmer, on days with both clear and overcast cloud conditions, than intermound soils (Canals et al. 2003). Contrary to previous findings, soil surface temperature at both Preston Park and Divide Mountain were warmer on undisturbed soils than on gopher eskers. It is probable that these differences in surface temperature are caused by sampling gopher eskers and not gopher mounds. Unlike agricultural areas and gopher mounds that are larger disturbances than gopher eskers and typically contain less vegetation, gopher eskers within the study sites contained substantial vegetation (as depicted in Figure 35) which could explain the reduction in surface temperature on eskers in this environment.

Subsurface soil temperature and soil moisture were dissimilar between undisturbed and gopher-disturbed sites at Preston Park but were equal at Divide Mountain. In a prairie landscape in Alberta, gopher burrowing activity did not appear to affect infiltration (Zaitlin et al. 2007), but this study appears to be an isolated instance. Most research suggests that gopher disturbance increases moisture infiltration on disturbed soils in a variety of environments (Reichman and Smith 1985; Laundre 1993; Kerley et al. 2004; Andelt and Case 2006). Undisturbed soils in Preston Park were significantly more moist than gopher-disturbed soils. A slight negative correlation was observed in undisturbed soils, where soil moisture increased slightly in less compacted soils. This is likely caused by the variable soil moisture detected throughout Preston Park. In forest soils, soil compaction and soil moisture are complex and highly variable depending upon a suite of localized soil characteristics (Adams and Froehlich 1981). Gopher-disturbed soils are less compact and are likely to experience more rapid moisture infiltration and drying than more compact, undisturbed sites. However, the rate at which gopher eskers dry following a precipitation event is unknown and likely requires several days before eskers become drier than the surrounding matrix. This is evident because gopher eskers at Divide Mountain were similar in soil moisture to undisturbed sites 48 hours after a precipitation event.

Olympic National Park

Although much research has examined the biology and social interactions of Olympic marmots (Barash 1973, 1989; del Moral 1984; Griffin et al. 2008; Griffin et al. 2009), little research has inspected the geomorphic effects of Olympic marmot burrows

on vegetation. At all three study sites in ONP, soils were significantly less compact on marmot-disturbed soils than on undisturbed soils. I am unaware of previous research examining soil compaction of marmot burrows, but these findings are consistent with soil compaction observed on gopher disturbances. Soil surface temperatures of marmot-disturbed soils were substantially warmer than undisturbed soils at both Blue Mountain and Obstruction Point. As noted above, previous research on gopher mounds has indicated that gopher mounds are typically warmer than adjacent, undisturbed areas. This appears to be true on Olympic marmot burrows. Most likely this is true because Olympic marmot burrows are large disturbances compared to gopher eskers (Figures 4 and 5) and consist of substantial exposed mineral soil, which is mostly free from vegetation. It is, therefore, not surprising that marmot-disturbed soils were warmer than undisturbed soils. Most marmot-disturbed soils also revealed a positive correlation between surface and subsurface temperatures. No difference in soil surface temperature between disturbed and undisturbed soils existed at Hurricane Ridge. Sampling at Hurricane Ridge consistently occurred under cloudy skies. Although previous research on gopher disturbances demonstrated that differences in soil surface temperatures between disturbed and undisturbed soils were significant on both clear and overcast days (Canals et al. 2003), this does not appear to be true of Olympic marmot-disturbed soils.

The differences in subsurface soil temperature and soil moisture were inconsistent between ONP sites. Blue Mountain and Obstruction Point showed no difference in subsurface soil temperatures between disturbed and undisturbed soils. Large areas of exposed mineral soil, indicative of Olympic marmot disturbances, are much warmer at the surface and it is likely that the large surface area allows for increased temperature

diffusion to lower soil depths. Consequently, the large nature of the marmot burrow results in surface and subsurface soil temperatures that are similar. Subsurface soil temperatures at Hurricane Ridge were likely significant between soil types because of the cloudy conditions. Soil associated with marmot disturbances was cooler below the surface than undisturbed areas, and it is possible that cloud cover prevented the exposed substrate from heating and creating a substantial thermal gradient within the disturbed soil. Hurricane Ridge and Obstruction Point exhibited similar soil moisture levels between soil conditions. Blue Mountain was substantially drier than the other locations and the vegetation of the area consisted of shorter fescue compared to Hurricane Ridge and Obstruction Point.

Hypothesis 3 - The Landscape Scale

H₀3: There is no difference in physical soil characteristics between Preston Park and Divide Mountain in GNP, nor is there a difference between Hurricane Ridge, Blue Mountain, and Obstruction Point in ONP.

Glacier National Park

Comparing Preston Park to Divide Mountain, both gopher-disturbed and undisturbed soils were statistically different. Undisturbed soils were substantially more compact at Preston Park than undisturbed soils at Divide Mountain whereas, gopher-disturbed soils were more compact at Divide Mountain and less compact at Preston Park. It has long been known that rainfall has the potential to increase soil compaction (Lull 1959 and references therein), yet compaction rates were higher at Divide Mountain 48

hours following a precipitation event. Soil compaction on undisturbed soils may be higher at Preston Park for two reasons. First, Preston Park represents the lower extent of the alpine treeline ecotone and contains more park-like, meadow environments which may attract more foraging activity of larger mammals (i.e. deer, bear, elk, bighorn sheep, mountain, goats. NPS n.d.) than Divide Mountain which represents the upper limits of the ecotone. Increased animal activity within Preston Park may result in increased soil compaction. Second, the parent material at Preston Park is glacial till, whereas Divide Mountain contains limestone parent material. Glacial till is characterized as being hard and compact, especially in areas containing streams (Rosenblatt et al. 2001), and may be the cause of the statistical difference. The more compact nature of gopher-disturbed soils at Divide Mountain is likely a result of early and more consistent exposure of eskers at Divide Mountain and less consistent exposure at Preston Park as previously described.

No differences in surface soil temperature existed between Preston Park and Divide Mountain for either soil condition. As mentioned above, gopher eskers in these environments contain a substantial amount of vegetation that grow on, and immediately adjacent to, gopher-disturbed soils and it is likely the vegetation which moderates the soil surface temperature on disturbed soils. Despite representing both the lower and upper limits of the alpine treeline ecotone, both study sites within GNP exhibited similar soil surface temperatures on undisturbed soils.

Olympic National Park

Sampling at ONP revealed that soil at Obstruction Point was significantly more compacted on both undisturbed and marmot-disturbed soil conditions than the other two

sampling locations. It is interesting to note that Obstruction Point contained denser fescue cover than Hurricane Ridge or Blue Mountain, and abandoned marmot burrows at Obstruction Point contained more grasses growing on the disturbed substrate than the other sites. Increased fescue cover provided a stabilizing effect on both soil conditions and resulted in higher compaction rates. The increased fescue cover also resulted in significantly cooler subsurface soil temperatures at Obstruction Point compared to Hurricane Ridge and Blue Mountain. The presence of vegetation is known to reduce the impacts of diurnal surface temperatures (Arya 2001) which are likely to propagate to subsurface levels. Subsequently, Obstruction Point had lower subsurface temperatures, but no significant difference existed in subsurface soil temperatures between sampling sites.

On undisturbed soils, Obstruction Point, which is more heavily dominated by fescue, revealed lower soil surface temperatures compared to Blue Mountain, which consisted of the least amount of fescue cover of the three ONP sites. Increased fescue cover resulted in cooler surface temperatures (Arya 2001). On marmot-disturbed soils, the highest surface temperatures occurred at Blue Mountain and were significantly warmer than both Hurricane Ridge and Obstruction Point. The lack of grasses on disturbed soils at Blue Mountain (Figure 5) exposed more mineral soil and allowed for warmer soil surface temperatures. Soil disturbed by gophers in Minnesota revealed high light levels similar to the early stages of succession (Inouye et al. 1987). It is likely these characteristics are true on marmot-disturbed soils in ONP, where marmot-disturbed soils result in increased light levels at the soil surface and increased surface temperature.

Soil moisture on both undisturbed and marmot-disturbed soils was highly variable between sites and resulted in statistical significance. Sampling conducted in ONP during August of 2010 occurred following a dry period of little precipitation. Furthermore, during the 10-days in the field, no precipitation occurred. Although the sites were similar in parent material, soil texture, and aspect, no knowledge of subsurface moisture flows was known at the time of sampling and may have affected the variability in subsurface moisture.

Hypothesis 4 - The Regional Scale

Hypothesis 4 (H_04) stated there is no difference in physical soil characteristics between GNP and ONP, and that both types of mammal disturbance have the same effect on substrate.

At the regional scale, several patterns were revealed. Soil compaction and both subsurface and surface temperatures on undisturbed soils were non-significant between GNP and ONP. Despite the fact that the sampling sites within the parks are separated by approximately 720 km, these soil variables on undisturbed substrates were very similar. The emphasis on sampling in two different parks that have similar climates, soil textures, vegetation, etc. ensured that the undisturbed matrix would be consistent between parks at the regional scale. All things being equal, there were significant differences in several variables when comparing mammal-disturbed soils between parks. Soil, for example, was significantly less compacted on marmot-disturbed soils than gopher-disturbed soils. These results solidify previous claims that the nature of mammal alteration to soil characteristics is broad and not consistent across species (Kerley et al. 2004). Logically,

the physiology and behavior of different fossorial mammals have diverse impacts on soil conditions. In GNP, gopher-disturbed surface soil conditions were cooler than marmot-disturbed soils. As previously mentioned, the larger disturbance created by the marmots expose greater mineral soil, contain less vegetation, and are, therefore, more likely to experience elevated soil surface temperatures comparable in value to those observed by Lauer and Klaus (1975).

The difference between subsurface soil temperatures on gopher and marmot-disturbed soils was slightly different with gopher disturbance being the warmer of the two disturbances. The reason for this warmer subsurface temperature on gopher disturbance, despite warmer surface temperatures and less soil compaction on marmot disturbance that should allow for the downward propagation of heat, is likely attributable to soil moisture. Gopher-disturbed soils were more moist than marmot-disturbed soils, and the increased heat capacity of the moisture may have facilitated warmer subsurface temperatures. Also, increased soil compaction, like that observed on gopher eskers, in forest nurseries is said to increase moisture retention (Lull 1959). Finally, precipitation events in GNP occurring during the field visits were likely responsible for the variation in soil moisture between undisturbed soils in both parks.

Hypothesis 5 - Chemical Soil Characteristics

H₀5: Chemical soil characteristics (pH, salinity, P, K, and organic matter) are the same in both areas of mammal disturbance and undisturbed areas.

Although some differences existed in P and K levels between undisturbed and disturbed soils, these differences may not have been sufficient to influence seed viability

and germination. Subalpine fir has been identified as a species that is not exacting in its soil requirements (Alexander et al. 1990), and although exposed mineral soil and moist humus provide the ideal seedbed (Alexander et al. 1984), subalpine fir can successfully germinate and survive on a diverse suite of seedbeds (Alexander et al. 1984 and references therein). More current work has suggested that subalpine fir is not particularly sensitive to fluctuations in soil chemistry (Calder et al. 2011). The slight acidity of soils sampled from GNP and ONP are consistent with soils associated with subalpine fir (Anderson et al. 1990), and contained only minor variability between undisturbed and disturbed soils. The inconsequential changes in salinity between soil disturbance types are unlikely to have an effect on a species that is often a pioneer species in harsh environments where typical associated species are unable to survive (Alexander et al. 1990 and references therein).

A reduction in organic matter on mammal-disturbed sites was the only consistent trend found by the laboratory analysis. Mammal-disturbed soils, which are less compact than the surrounding matrix, may facilitate gas exchange with the atmosphere (Kirschbaum 1995) and may accelerate the decomposition rate of organic matter. Increased gas exchange may have an effect on seed viability and germination. Furthermore, organic matter has a positive effect on available water capacity (Hudson 1994) and may improve seedbed conditions.

Hypothesis 6 - Seed Germination

Hypothesis 6 (H₀₆) stated that if climatic variables were standardized, subalpine fir germination would be the same in both disturbed and undisturbed soils.

Seed germination within soil type and at different scales highlighted several differences. At the local scale, no difference in germination existed at Preston Park or Divide Mountain between undisturbed and gopher-disturbed soils. In ONP, Hurricane Ridge and Obstruction Point showed no difference in seed germination between undisturbed and marmot-disturbed soils, but Blue Mountain revealed a significant preference for seed viability and germination in disturbed soils. Similar findings existed at the landscape scale, where no differences existed in seed germination within GNP but seeds did significantly better on disturbed substrate within ONP. Interestingly, at the regional scale, the preference for seed viability and germination in disturbed soils became increasingly apparent. Exposed mineral soil, which is more characteristic of marmot disturbance than gopher disturbance, has been cited as a substrate free of competition and therefore, an optimal substrate for spruce in boreal forests (Greene et al. 1999). Soil disturbed by gophers in Minnesota revealed relatively low levels of nitrogen but high light levels one would expect in the early stages of succession (Inouye et al. 1987). It is likely these conditions are also true on marmot-disturbed soils in ONP where marmots disturb soils, increase light levels at the soil surface, and develop soil conditions similar to early succession, which are favorable substrate for subalpine fir seeds. Furthermore, spruce germination and emergence on substrate that was manually disturbed to expose mineral substrate reported that disturbance was the primary factor affecting seedlings (Munier et al. 2010). Although the manual disturbance may represent disturbance caused by fossorial mammals, manual disturbance is overly simplistic and does not account for the physical and chemical nuances associated with actual fossorial mammal activity. Despite the manual disturbances not representing actual mammal disturbances, spruce

emergence was enhanced by disturbed substrate (Munier et al. 2010). Forbis et al. (2004) stated that gopher-disturbed areas older than five years exhibited higher seedling establishment than surrounding areas, and concluded that several years were required to reestablish a sufficient seed bank in disturbed areas. Although the research by Forbis and colleagues (2004) did not address conifer seedlings, a similar scenario is likely for conifers on mammal disturbances. Although no research exists for the duration of marmot burrows on the landscape, it has been noted that burrows persist for multiple years (Griffin et al. 2008; Griffin et al. 2009) and the longevity of marmot disturbances, compared to the relatively rapid decay of gopher eskers (Butler and Butler 2009; Knight 2009), may provide sufficient time for a seedbed to establish and conifers to germinate and emerge.

Despite the many obvious advantages that mammal disturbance, particularly marmot disturbance, appear to offer conifer germination, some aspects of mammal disturbance may be detrimental to conifers beyond germination. One such factor is the decreased organic matter observed in all disturbed soils compared to undisturbed soils. Less compact soils associated with disturbance have increased gas exchange with the atmosphere (Kirschbaum 1995) and may increase the decomposition of organic matter. Organic matter has a positive effect on available water capacity within many soil types (Hudson 1994), and the less compact nature of mammal-disturbed soils may allow more rapid infiltration, but may not have the ability to retain moisture within the surface to the 10cm depth that encompasses the environment for conifer germination, emergence, and seedling survival (Schütz 2005). Moreover, although marmot disturbances appear to be beneficial to germination, the decreased moisture holding ability of the disturbed soil

coupled with the high temperatures may desiccate newly germinated seeds and prohibit them from becoming established.

Erosion of gopher eskers in GNP may hinder seed viability and germination. Butler and Butler (2009) concluded that gopher eskers in Colorado disintegrated in less than one year and the sediment associated with the eskers rapidly dispersed. The authors suggested that the dispersal of esker sediment may accumulate in neighboring areas and provide amenable conditions for conifer seedling establishment. Knight (2009) found that gopher eskers in Washington disintegrated within a matter of weeks following exposure from melting snow. Contrary to Butler and Butler, Knight suggested that the fine sediment used by gophers for esker creation was highly susceptible to both eolian and fluvial mass-wasting processes and was capable of being transported great distances. Despite the rapid decay of eskers following exposure in the spring, it is known that the gopher-disturbed sites at Preston Park in this study have been continually disturbed by gophers for several years. Continual disturbance may prohibit successful germination and establishment of conifers. Schütz (2005) did not examine subsurface impacts of gophers on conifer seedlings and was, therefore, unable to attribute seedling damage to gopher activity. If gopher activity is detrimental to seedlings, a temporal lag may explain the visual observation of young seedlings in disturbed areas but no saplings or juvenile trees. Seedlings may establish in areas where disintegrated eskers have resulted in a redistribution of loose sediments (Butler and Butler 2009), or seedlings may potentially act as interceptors of loose sediment being transported by erosional processes and may create an abundance of accumulated sediment for future esker use. Additional research is needed to evaluate these possibilities.

Areas of the alpine treeline ecotone disturbed by fossorial mammals are significantly different from undisturbed areas. Gopher and marmot activity reduce soil compaction and such sites were typically drier than adjacent undisturbed soils. Soils disturbed by gophers in GNP were surprisingly cooler than undisturbed soils. These findings are contrary to previous findings examining temperature of soil associated with gopher disturbance. It is probable that these differences in surface temperature are because of specific sampling of gopher eskers and not gopher mounds which have been included in previous studies. Gopher eskers contained substantial vegetation on the actual esker and immediately adjacent to eskers, which likely explains the reduction in surface temperature on eskers in this environment. On marmot-disturbed soils in ONP, soil temperatures were warmer than on undisturbed soils. These findings echo the conditions cited for gopher disturbance. The large size and longevity of gopher disturbances on the landscape expose mineral soils that are susceptible to increased solar radiation and result in higher temperature. Subsurface soil temperature was more variable and was associated with soil moisture. Localized precipitation and unknown variables associated with subsurface moisture flow are likely to blame in complex, heterogeneous mountain environments. Additional research is required to improve understanding of moisture variability within the top 10cm of mammal-disturbed soils in alpine environments.

Soil texture and chemical soil properties were surprisingly consistent between undisturbed and disturbed soils and were fairly consistent between national parks. The only discrete pattern that developed from the soil analysis was a consistent decrease in organic matter in disturbed soils. Decreased organic matter may result in less moisture

retention, which may be detrimental to long-term establishment of trees within this environment. Seed germination was higher on marmot-disturbed soils than on gopher-disturbed soils. Despite these experimental findings, no statistical difference existed in seed germination within control soils compacted to gopher and marmot rates observed in the field. It is likely, therefore, that although soil compaction appears to influence soil moisture and soil temperature, it may not be the ultimate driving cause determining seed germination in mammal-disturbed soils. Additional research is needed to evaluate individually these variables in an effort to identify how fossorial mammals affect seed germination and treeline dynamics in an alpine environment.

In the context of niche theory, this research provides some important insights into the concept of regeneration niche and the belowground requirements necessary for successful germination. Although successful germination of subalpine fir seeds occurred in marmot-disturbed soils and marmot-disturbed substrates had significantly higher levels of germination than gopher-disturbed soils, observations from the field revealed few seedlings growing on marmot disturbances. In some environments, it has been observed that apparently suitable sites are lacking both seeds and seedlings of typical species, therefore suggesting that seed limitation is a common problem (Clark et al. 1998). Because plants are unable to distribute seed to all locations in which the plant is ideally adapted for survival, many species that are less ideally adapted are able to establish (Hurtt and Pacala 1996; Turnbull et al. 2000). The relatively large size of subalpine fir seed (average of 76,720 seeds per kilogram; Alexander et al. 1990) results in low dispersal capability. In Colorado, approximately fifty percent of Engelmann spruce and subalpine fir seeds land within 30m of windward sources (Noble and Ronco 1978). It is

likely, therefore, that subalpine fir seed is unable to adequately distribute to all marmot disturbances and seed limitation is a controlling factor. Climate change may alter wind speeds and marmot disturbances may be more important to conifer establishment under future climate scenarios.

The differences in chemical soil characteristics between study locations may explain some of the variation observed in seed germination. It has been suggested that growth rates of seedlings are more responsive to differences in soil fertility than growth rates of larger, more mature trees (Reich 1998), and this may be true of germinating subalpine fir seeds as well. In conifer nursery environments, it has been suggested that the optimum pH for conifers is between 5 and 6 (Tinus 1980). With the exception of the greenhouse control soil, the pH values of soil samples obtained within the national parks were primarily within this range. Only slight deviations above and below pH values of 5 and 6 were observed in soil samples collected at the national parks. Previous research has shown that pine germination and growth was enhanced in acidic soils as compared to more basic soils (Redmann and Abouguendia 1979). The consistent pH of undisturbed and disturbed soils from both national parks suggests that pH is not the major controlling factor of seed germination on mammal-disturbed substrates.

A portion of phosphorous available for plant uptake in *Abies* forests is the result of organic matter decomposition and mineralization (Powers and Edmonds 1992). The cool climates of the study sites within Glacier and Olympic National Parks retard the decomposition of organic matter and may be responsible for the low levels of P observed throughout the study sites. However, no consistent trends of P were evident from the soil analyses and it is unlikely that P is the driving force of germination. It is more likely that

organic matter affects moisture as noted by silvicultural practices which claim that organic matter preservation and the prevention of soil compaction improve soil moisture and aeration conditions (Fowells and Means 1990). On sandy, forest nursery soils with low pH, K can be depleted rapidly by leaching (Krause 1965). Less compacted soils associated with gopher and marmot disturbance may exhibit higher rates of leaching than undisturbed soils. This may have caused lower levels of K observed on all mammal-disturbed soils except Blue Mountain, ONP. The differences, however, in K between undisturbed and disturbed soils, were generally minimal (Table 19) and it is, therefore, unlikely that fossorial mammals examined in this study had an impact on soil potassium.

The underlying bedrock and surficial geology of the study sites are more likely the cause of elevated K at Preston Park, GNP, as well as Hurricane Ridge and Blue Mountain, ONP. The optimum levels of soil nutrients for many conifer species are unknown (Fowles and Means 2000). In the mountains of Colorado, forest communities comprised of quaking aspen and Engelmann spruce/corkbark pine grew on a variety of bedrock geologies containing different underlying nutrients, yet forest stands demonstrated similar bulk foliar chemistries across parent materials, suggesting that foliar concentrations were poor estimators of nutrient levels (Castle and Neff 2009). It is probable, therefore, that surficial geology and surface soil nutrients are more representative of tree requirements than subsurface geology. Preston Park, GNP, contains substantial glacial till from the late Pleistocene which is comprised of material from the Belt Supergroup (Carrara 1990). The conglomeration of glacial material may contain more feldspar than the limestone parent material at Divide Mountain, GNP, which may explain the higher levels of potassium observed at Preston Park. The same

appears to be true in ONP, where less argillite at Obstruction Point resulted in lower levels of potassium.

Although potassium has been identified as an important nutrient for conifer growth (Tripler et al. 2006 and references therein), less is known about the impact of K on subalpine fir germination. In a laboratory setting, germination of several native plants of the United States benefited from briefly soaking seeds in potassium hydroxide (Luna et al. 2009). High concentrations of potassium hydroxide, or extended periods of soaking, however, have been shown to be detrimental to germination (Goa et al. 1998). The amount of potassium at Preston Park, GNP, may be higher than optimal germination requirements for subalpine fir and subsequently, more germination may have occurred at Divide Mountain, GNP, where K was lower, albeit, the differences in germination were non-significant.

The results from this research demonstrate that fossorial mammal disturbance can be perceived as a process creating potential nurse sites, similar to those described by Pérez (2002), Flores and Jurado (2003), Resler et al. (2005), and Resler (2006), and can influence local pattern and process at alpine treeline. The importance of fine-scale processes on treeline dynamics has been studied extensively in past decades, as cited above, and much research has attempted to identify the impact of individual fine-scale processes. Disturbance by fossorial mammals now joins the ranks of many fine-scale geomorphic processes at alpine treeline (Butler et al. 2009), that have potential to affect conifer germination and establishment. As demonstrated above, the effects of mammal-induced soil compaction greatly influence microclimatic variables and chemical soil properties. These microclimatic changes and soil alterations created by differences in

soil compaction, facilitated conifer germination on disturbed soils and are reminiscent of local site characteristics associated with boulders and areas of turf-exfoliation, which have been suggested and shown to increase seedling establishment (Butler et al. 2004; Resler et al. 2005; Resler 2006). It is clear that fine-scale disturbances, whatever they may be, can have substantial impacts on treeline dynamics.

This research has stated that reduced soil compaction by fossorial mammals affects microclimate and soil characteristics and has potential to increase conifer seed germination. An important aspect of this modification involves solar radiation. In Wyoming, Germino et al. (2002) stated that the occurrence of seedlings and saplings above alpine treeline was less common with increased distance from tree islands and large trees. Seedlings that emerged in exposed soils located away from mature trees did not survive because of greater sky exposure. In Ecuador, similar findings were observed. Bader et al. (2007) stated that above treeline, seedlings that established far from neighboring trees were subject to high mortality. At the lower extent of the alpine treeline ecotone, trees were more likely to survive because of shady environments created by neighboring trees. The authors stated that photoinhibition was the controlling factor of treeline in that region of Ecuador.

It is obvious that excessive exposure to radiation at treeline environments can result in photoinhibition and have a negative impact on the location of juvenile conifers. Despite this fact, photoinhibition occurs in the leaves of juvenile trees and appears to be problematic for emerged seedlings, and not necessarily seed germination. Some work has suggested that the germination of conifer seeds is slightly sensitive to varying levels of light early in the germination phase, but the importance of light decreases with time

(Harrington 1977). In this study, photoinhibition may partly be responsible for the low number of seedlings observed growing on exposed gopher and marmot disturbances within the study areas. The purpose of this study, however, was to assess the effects of soil compaction on germination, and it is unlikely that radiation is the primary determinant of germination, as seeds germinate several millimeters below the ground surface level.

Although high levels of radiation are ubiquitous in alpine environments, this research tends to suggest that mammal disturbance, primarily the effects of soil compaction on physical and chemical soil characteristics, can create a nurse site that is more amenable to seed germination than undisturbed areas. Subalpine fir may have more selective germination requirements than other species (Germino et al. 2002), and mammal disturbance may provide the specific requirements necessary for germination. Furthermore, mammal disturbance, as indicated by this study, has potential to radically alter soil moisture and soil nutrients, neither of which were assessed by Bader et al. (2007) who cited photoinhibition as the driving force of treeline. Previous empirical evidence suggests that photoinhibition is important in the development of treeline pattern, however, future studies of alpine treeline need to recognize the importance of fossorial mammal disturbances on treeline dynamics and incorporate this element into future work.

The findings of this research highlight and enhance understanding of conifer dynamics in alpine environments and provide insight into how conifer germination may be influenced by fossorial mammals. Previous research has noted that mammal disturbances modify soil characteristics and modify vegetation (Forbis et al. 2004), but other than one study on *Artemisia* (Berlow et al. 2002), I know of no work that has

attempted to evaluate quantitatively possible associations between fossorial mammal disturbance and woody species germination in alpine environments. Furthermore, these findings suggest that fossorial mammal disturbance can have different consequences on conifer germination. The plethora of fossorial mammals in alpine environments, therefore, merits evaluation to determine the individual effects of fossorial mammal disturbance on conifer dynamics.

From a theoretical perspective, this research is important because it emphasizes the interface between ecological and geomorphic patterns and processes. The interface between ecology and geomorphology has received much debate in recent years (Fonstad 2006; Stallins 2006; Post et al. 2007; Renschler et al. 2007; Reinhardt et al. 2010; Osterkamp et al. 2012), and many scientists have stressed the importance of involving both disciplines in an attempt to identify linkages between Earth systems (Paola et al. 2006; Murray 2009; Dadson 2010). The results from this research imply that soil modification by a zoogeomorphic agent can influence ecological process and demonstrates the need for additional research and understanding at the ecology-geomorphology interface.

Finally, the findings of this research bring into question how fossorial mammal disturbances may impact conifer germination under future climate scenarios. As noted by Butler (2012), climate change has the potential to modify the effect of fossorial mammals at treeline. Under warmer conditions, marmot-disturbed environments may become too hot for initial seed germination despite the exposed mineral soils which are less compact and free of interspecies competition. Conversely, warmer temperatures may enhance gopher-disturbed substrate and result in increased germination and survival.

Changes in precipitation may also facilitate advancement into disturbed soils. Despite the advancements this research elucidates in understanding conifer germination on mammal-disturbed soils in alpine environments, additional research is needed to evaluate the effects of different fossorial mammals and evaluate how impending climate change will further influence and modify fossorial mammal/alpine conifer dynamics at the ecology and geomorphology interface.

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VITA

Clayton James Whitesides grew up in the mountains of northern Utah where he spent his time snow skiing and fly-fishing. Following his graduation from high school, Clayton lived in northeastern Brazil for two years and upon return to the United States, attended Utah State University in Logan, Utah where he played racquetball for the USU club team. While attending USU, he worked as a physical geography teaching assistant and a cartographer for the Federal Highway Administration's National Scenic Byways Program. Clayton also studied abroad at the Tecnológico de Monterrey in Mazatlán México prior to his graduation from Utah State with the Bachelor of Science degree in Geography in 2006. Upon completion of his undergraduate education, Clayton attended Brigham Young University where he worked as a teaching assistant for several geography courses. Clayton earned the Master of Science degree in Geography from BYU in 2008. In the fall of 2008, he entered the Graduate College of Texas State University-San Marcos, where Clayton conducted research for his Ph.D. in Environmental Geography.

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