Climate change impacts on the distribution and performance of plant species at Mount Rainier

Kevin R. Ford

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Reading Committee:
Janneke Hille Ris Lambers, Chair
Thomas M. Hinckley
Abigail Swann

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Abstract

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Chair of the Supervisory Committee:
Dr. Janneke Hille Ris Lambers
Biology

Ongoing anthropogenic climate change has profound implications for species, communities and ecosystems around the world. Yet climate is only one of many important drivers in ecological systems, with topography, soils, disturbance, ontogeny, biotic interactions, land-use and many other factors also playing key roles. To produce useful predictions of climate change impacts that can inform conservation actions, we must first develop an understanding of how climate interacts with other components of the environment to influence ecological dynamics.

In this dissertation, I have attempted to identify important interactions of climatic and non-climatic factors that have the potential to surprisingly alter the ways climate change influences the distribution and performance of plant species at Mount Rainier National Park. In Chapter 1, I begin by reviewing some of the important ways climate change is likely to impact Mount Rainier, finding that while the Park's resources will likely be imperiled, Mount Rainier will also become increasingly important for preserving the region's biodiversity because of its

relative lack of other pressures (e.g., habitat destruction) and high elevation lands that can serve as refugia for cold-adapted species. Chapter 2 describes observed patterns in climate (temperature and snow disappearance date) at coarse and fine spatial scales, showing that climate can vary as much at fine scales (tens of meters) due to differences in vegetation structure and topography as it does at coarse scales (thousands of meters) due to differences in elevation and exposure to storm tracks. These results imply that some species may only have to migrate small distances to track suitable climate during periods of climate change, which may buffer them from its negative impacts. Chapter 3 presents results from a study in Mount Rainier's subalpine and alpine meadows which found that the interaction of climate and soil constraints on seedling establishment during climate change may cause the range of the meadows to contract at their lower limit faster than they expand at their upper limit, a result that would not be expected from considering climate alone. Chapter 4 includes analyses of tree growth across elevation at Mount Rainier which suggest that the relationship between climate and growth changes with tree size in a species-specific manner, implying that forest responses to climate change will be complex. I end with a synthesis summarizing major findings and suggesting avenues for future research.

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Chapter 1: Overview of the impacts of climate change at Mount Rainier National Park

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Summary

Past and future climate change

Average annual temperature in the Pacific Northwest has increased 0.83ºC (1.5ºF) since 1920 and is projected to increase an additional 2.0 - 4.0ºC (3.6 - 7.2ºF), or more, by the end of the century. In addition to higher temperatures, the region will likely experience wetter winters and drier summers, with a slight increase in annual precipitation. These alterations of the climate system are due in large part to human actions, namely the emission of greenhouse gases. Below are some of the ways Mount Rainier National Park could be affected by these changes in climate.

Glaciers, debris flows and floods

The Park's glaciers have decreased in area and volume over the last century in association with increasing temperatures. The retreat of the glaciers has exposed large amounts of loose soil that can be washed into river channels during heavy rain events. Once in the channel, this soil can mix with water to form a fast-moving slurry called a debris flow. These flows can be very powerful and dislodge large boulders or trees, and also destroy riverside buildings and roads. Much of the debris washed into the Park's rivers settles out at lower elevations and accumulates on the river bed. Some areas of the Park have experienced such high rates of accumulation that the beds of some stretches of river are actually above the surrounding landscape, making it more likely for waters to overtop river banks and flood large areas of land during intense rainstorms. For example, Longmire is 8.8m (29 feet) *below* the bed of the nearby

Nisqually River. Future temperature increases will likely lead to greater retreat of the glaciers and perhaps increased risk of debris flows and flooding.

Air quality

Mount Rainier's location downwind of the Seattle-Tacoma metropolitan area can lead to high concentrations of air pollutants in the Park. In fact, high elevation sites such as Paradise often have higher average ground-level ozone concentrations than Seattle. Ground-level ozone is an air pollutant that harms humans and other organisms. Higher temperatures tend to lead to higher concentrations of ground-level ozone and other air pollutants. Therefore, future warming is expected to have a negative impact on the Park's air quality. However, pollutant concentrations are also strongly affected by emission rates, making it difficult to predict future levels of air pollution.

Forests

The abundances and distributions of the Park's tree species are strongly correlated with climate. Thus, climate change is expected to lead to shifts in the geographic ranges of tree species within the Park. However, non-climate factors also influence species distributions, so species response to climate change will likely be complex. In addition, the long lifetimes of these trees suggest that climate change induced range shifts will be slow in the absence of major disturbances. But background rates of tree mortality have increased in Pacific Northwest forests, a trend thought to be caused by higher temperatures and greater drought stress. This increased mortality could alter the structure, composition and productivity of Mount Rainier's forests. Also, the increased temperatures and decreased summer precipitation brought about by climate change would lead to drier conditions that could increase the frequency of forest fires. An increase in fire frequency could also lead to faster shifts in tree species ranges if fires kill adult members of cool-adapted species to allow seedlings of warm-adapted species to establish.

Subalpine and alpine meadows

The subalpine and alpine meadows of the Park are found at high elevations where temperatures are too cold or snow covers the ground for too long for trees to grow. Over the last century, ecologists have documented tree establishment in subalpine meadows throughout the Park in association with increased temperatures. Higher temperatures and longer snow-free periods in the future will likely lead to the establishment of more trees in subalpine meadows and colonization of bare ground by alpine plants, leading to an overall upward movement of these meadows. This movement will probably result in a reduction of the area occupied by the meadows, because there is less land at higher elevations, which could lead to the loss of some subalpine and alpine plant species.

Species at risk

Virtually all of the species Mount Rainier supports will be affected by climate change in some way. Many of these species will likely be at risk of decline within the Park and throughout their range. Below, I discuss two species that could be in jeopardy. These case studies exemplify the risks species face and the complexities of predicting species responses to climate change.

Whitebark pine

The whitebark pines at Mount Rainier have been victim to a non-native disease called the white pine blister rust that has killed many of these trees in the Park. Climate change poses additional threats to this already imperiled tree species. One of these threats is a potential increase in outbreaks of the mountain pine beetle (a bark-boring insect) which can cause widespread mortality amongst whitebark pines. Although the mountain pine beetle is native to the Park, the high elevation habitats of whitebark pine have historically been too cold for beetle populations to reach epidemic proportions in most years. Rising temperatures would lead to whitebark pine stands becoming more suitable for the beetle, which could, in turn, lead to more beetle outbreaks and reduced numbers of whitebark pines.

The American pika

The American pika is a small mammal found at high elevations in the Park. The animal is sensitive to high temperatures and could be negatively affected by warming in parts of its range. Consistent with this expectation are observations in the Great Basin region of the Southwestern US that 10 out of 25 pika populations documented in the 20th century have apparently disappeared and that the extinct populations were in warmer locations than surviving populations. However, pikas currently occupy locations with a wide range of average temperatures, suggesting that a large portion of the species' habitat will continue to experience suitable temperatures even with substantial warming. Pikas have also been known to adjust their behavior to cope with high temperatures by resting inside shady boulder fields during hot weather and shifting their foraging to cooler times of day. Thus, the pika will likely face threats from climate change, but might be well suited to cope with these threats.

Introduction

"Warming of the climate system is unequivocal, as is now evident from observations of increases in global average air and ocean temperatures, widespread melting of snow and ice, and rising global average sea level."

-Intergovernmental Panel on Climate Change (IPCC 2007)

Average annual temperature in the Pacific Northwest has increased 0.83ºC (1.5ºF) since 1920 and is projected to increase an additional 2.0-4.0ºC (3.6-7.2ºF), or more, by the end of the century. In addition to higher temperatures, the region will likely experience wetter winters and drier summers, with a slight increase in annual precipitation (Mote and Salathé 2009). The scientific consensus is that these changes in climate are due in large part to human actions, namely the emission of greenhouse gases from burning fossil fuels, deforestation and agriculture (Mote and Salathé 2009, IPCC 2007). The purpose of this report is to review how these ongoing changes are affecting some of the most valued resources at Mount Rainier National Park and what these changes mean for the future of the Park. It appears that a number of these resources are vulnerable to large changes in climate and that the Park will face unprecedented challenges in conserving the resources it is mandated to protect.

Glaciers, debris flows and floods

Mount Rainier's glaciers are the largest single-mountain glacier system in the contiguous 48 states (91 square kilometers or 35 square miles), represent 25% of the total ice area in the contiguous 48 states and contain as much ice (by volume) as all the other Cascade volcanoes combined (NPS 2001, Nylen 2004). However, these glaciers shrank 22% by area and 25% by volume between 1913 and 1994 in conjunction with rising temperatures (Nylen 2004). The most recent studies of Park glaciers have shown that monitored glaciers are continuing to retreat (NPS 2009a). Beyond Mount Rainier, there has been a general trend of glaciers shrinking across western North America (Moore et al. 2009) and the globe (Lemke et al. 2007) over the last century, in association with increasing temperatures.

This shrinking not only diminishes the Park's iconic glaciers, but also increases the risk of geologic hazards. As the glaciers recede, they expose and de-buttress large amounts of soil that is easily washed into river channels during heavy rain events (Figure 1). During especially intense rain events, this large amount of soil can mix with water in river channels to form a fast-moving slurry called a *debris flow*, which is similar in appearance to wet concrete. The mass of the soil adds momentum to the river's flow and makes it much more powerful than it would be with water alone. As a result, the debris flow can dislodge large boulders, old-growth trees and other large objects in its path as it moves down steep slopes, leading to a snowball effect where the flow becomes more powerful and mobilizes even more debris (Ballantyne 2002). These debris flows pose a threat to human infrastructure in the Park, and can easily destroy riverside buildings and roads.

As the debris flows travel down river and reach the Park's lower elevations, the slope of the river's course becomes less steep and the river's flow slows down. As this happens, the soil, rocks and other objects in the debris flow settle out and begin to accumulate in the riverbed, increasing the height of the channel in a process called *aggradation*. Because of the large amount of loose soil exposed by glacial recession in the Park, substantial aggradation occurs even during periods of normal river flow. However, aggradation is especially rapid during debris flows spawned by heavy rains. For example, the background rate of aggradation is 15 – 36 cm (6-14 inches) per decade in the Park's braided rivers, but around 1.8m (6 feet) of material was deposited along a section of the Nisqually River during a single debris flow. In other words, around 30 – 70 years' worth of background aggradation occurred in the span of a few days (Beason and Kennard 2007).

High rates of aggradation can raise river channels to elevations above the nearby landscape, so that one actually has to walk *up*hill to reach the river. For instance, the bed of the White River is as much as 4.8m (16 feet) above the adjacent landscape which includes State Route 410 (an important highway for Park workers and visitors), while the bed of the Nisqually River is 8.8m (29 feet) above Longmire (one of the largest developed areas in the Park containing lodging, offices and facilities for workers and visitors). Because of the elevated of river channels, floods tend to be more severe because water can more easily spill over river banks and down onto the surrounding landscape during high rainfall events (Beason and Kennard 2007).

Mount Rainier experienced how damaging these hazards can be in November 2006 when a major storm produced 46cm (18 inches) of rainfall in just 36 hours (NPS 2009b). The debris flows and floods that ensued caused widespread damage throughout the Park, including destroyed roads, trails, campgrounds, buildings and utility systems (NPS 2009b). The damage forced the Park to close for 6 months and total recovery costs have been estimated at over $27 million (NPS 2009b). Although extraordinarily high rainfall set off the debris flows and flooding, receding glaciers probably made these hazards more destructive than they would have been otherwise (Beason and Kennard 2007).

Heavy rainfall is not the only force that can spark these debris flows and floods. As glaciers melt, large lakes can form on top of or within the glaciers, held in place by ice dams. These ice dams can eventually fail, releasing large amounts of water in a *glacial outburst flood* (also known by the Icelandic term, *jökulhlaup*). Ice dam failures can be brought about by periods of high rainfall or high temperatures when a large amount of meltwater is produced (Walder and Driedger 1993). These floods can then spawn debris flows, creating serious threats to downstream locations. Glacial outburst floods have occurred repeatedly within a number of the glacier fed streams and rivers of Mount Rainier (Walder and Driedger 1993). A similar phenomenon can occur when lakes form behind the terminal moraine of a receding glacier. The moraines, which serve as dams for the lakes, can fail and unleash large outburst floods that lead to debris flows downstream. These types of floods have occurred in several valleys that have experienced glacial recession in western North America (Moore et al. 2009).

As the climate continues to warm, the glaciers of Mount Rainier will likely continue to recede. This would lead to more unstable soil becoming exposed, likely increasing the frequency and intensity of debris flows (O'Connor and Costa 1993, Evans and Clague 1994). In addition, the newly exposed soil will probably lead to greater increases in the rate of aggradation within Park rivers, further increasing the risk of flooding (Beason and Kennard 2007). Thus, climate change poses a serious threat to the glaciers, rivers, infrastructure (including buildings and roads that are part of the Mount Rainier National Historic Landmark District) and people of Mount Rainier.

Air quality

Mount Rainier National Park is a mandatory class 1 air quality area as defined by the Clean Air Act, which means the Park receives the highest level of air quality protection. Air pollution mostly comes from outside Park boundaries, particularly from the Seattle-Tacoma metropolitan area. Air pollutants that have been noted as a concern for the Park include ground-level ozone, sulfates, nitrates and fine particulates (NPS 2001). The concentration of some of these pollutants may be altered by climate change.

Ground-level ozone

Although ozone in the stratosphere is important for protecting humans and other organisms from damaging ultraviolet radiation, ozone produced near the surface of the Earth can have negative impacts on human health and ecosystem function. For humans, high concentrations of ozone can cause both short and long term declines in lung function (Bernard et al. 2001). Individuals working and exercising outside as well as those with respiratory illnesses are especially at risk (Bernard et al. 2001). In addition, ground-level ozone is thought to be responsible for over 90% of the damage to vegetation caused by air pollution because it disrupts photosynthesis (Felzer et al. 2004).

Ground-level ozone is formed in the atmosphere by the reaction of nitrogen oxides with volatile organic compounds in the presence of sunlight. Nitrogen oxides are emitted from natural sources such as lightning and biological processes in the soil, as well as from human sources, mostly the combustion of fossil fuels. Similarly, volatile organic compounds come from natural sources such as vegetation, and from human sources including gasoline, refineries, chemical plants, factories and various commercial products (e.g. paint, cleaning supplies, pesticides) (Bernard et al. 2001). Thus, although ground-level ozone is produced in natural environments, it reaches far higher concentrations because of industrial activities.

In the past few decades, elevated ozone concentrations have been recorded within the Park, particularly at high elevation sites such as Paradise (NPS 2001, Brace and Peterson 1998, Peterson et al. 1999). In fact, high elevation sites at Mount Rainier typically have greater average concentrations of ozone than the Seattle-Tacoma metropolitan area and have experienced some of the highest average concentrations of ozone in western Washington. These high concentrations are thought to result from prevailing winds carrying ozone and its precursors from urban areas in the Puget Sound Region to Mount Rainier (Peterson et al. 1999, Cooper and Peterson 2000). Although the Pacific Northwest does not have the highest levels of ozone pollution in the country (EPA 2006), recent decades have seen ozone levels in the region rise above standards set by the US Environmental Protection Agency (EPA) (Barna et al. 2000). Several species of plants in the Park have been shown to be sensitive to ozone pollution (Brace et al. 1999) and vegetation within the Park, particularly at high elevations, is thought to be at risk of ozone damage given current concentrations (Brace and Peterson 1998).

Climate change is expected to increase concentrations of ground-level ozone in the Pacific Northwest and other regions because high concentrations of ozone are correlated with high temperatures (Bernard et al. 2001, Peterson et al. 1999, Confalonieri et al. 2007, Jackson et al. 2009, Chen et al. 2009). This correlation exists because higher temperatures increase the rates at which nitrogen oxides and volatile organic compounds react in the atmosphere to form ozone, and also increase natural emissions of nitrogen oxides (from the soil) and volatile organic compounds (from vegetation) (Bernard et al. 2001).

However, it should be noted that regional ozone concentrations have declined in the last decade (Jackson et al. 2009) and more stringent air quality standards regarding ground-level ozone have been imposed (EPA 2008). But climate change, growing human populations and expanded industrial activity may detract from or override these improvements. For example, ground-level ozone pollution has been projected to increase by 28% by mid-century in King County Washington (based on the IPCC A2 emissions scenario, which assumes high rates of greenhouse gas emissions) (Jackson et al. 2009). Changes in pollutant emissions in nearby metropolitan areas have the potential to impact air quality in the Park since ozone and its precursor pollutants can travel hundreds of kilometers from their source and most of the Park's air pollution comes from the Puget Sound region (NPS 2001, Bernard et al. 2001). Thus, although predicting future levels of ground-level ozone is difficult, climate change will likely tend to increase the problem of ozone pollution.

Sulfates, nitrates and acid deposition

Levels of sulfates and nitrates are of concern to the Park because they are associated with deposition of sulfuric and nitric acids, pollutants that increase the acidity of terrestrial and aquatic environments. Increased acidity in terrestrial ecosystems can disrupt soil chemistry and decrease plant growth and vigor, while increased acidity in aquatic systems can lead to reductions in populations of fish and other organisms (Miller 2002). Past measurements at Mount Rainier have found high sulfate levels relative to other Parks in the Pacific Northwest and increasing levels of nitrates (NPS 2001). In fact, some of the lowest pH (highest acidity) readings in the state have been observed at Paradise (NPS 2001).

Acid deposition is driven mostly by the combustion of fossil fuels, which results in the emission of sulfur dioxide and nitrogen oxides into the atmosphere (though there are smaller, natural sources of sulfur dioxide and nitrogen oxides) (Bernard et al. 2001). In the atmosphere, the sulfur dioxide and nitrogen oxides react with oxygen and water vapor to form sulfuric and nitric acids (which contain sulfates and nitrates, respectively). These acids and their precursors can be transported hundreds of kilometers from their sources (Miller 2002).

Climate change is expected to increase rates of acid deposition because rising temperatures will tend to accelerate the rates at which sulfur dioxide and nitrogen oxides are converted to sulfuric and nitric acids which will increase the potential for acid deposition

(Bernard et al. 2001). However, there are many factors that affect acid deposition (including economic and regulatory trends), which makes predicting the direction and magnitude of changes in acid deposition difficult.

Fine particulates

Fine particulates are of concern to the Park because they decrease visibility (NPS 2001) and have the potential to harm human health by negatively impacting the respiratory system (Bernard et al. 2001). However, there is limited evidence available about the effects of climate change on fine particulates, preventing any clear conclusions about how climate change may impact fine particulate concentrations in the Park (Jackson et al. 2009).

Forests

Forests occupy about 60% of Mount Rainier National Park and span an elevational range from around 500m (1640 ft) to approximately 1800m (5900 ft) (Franklin et al. 1988). However, the species of trees that make up these forests differs drastically at different elevations. Lower elevation forests are dominated by Douglas fir, western hemlock and western red cedar, while higher elevation forests are mainly composed of Pacific silver fir, mountain hemlock and Alaska yellow cedar (Franklin et al. 1988). The elevational stratification of tree species likely exists because species that perform better in cooler environments dominate high elevation sites, while species that perform better in warmer environments dominate low elevation sites, as species abundance tends to vary predictably with temperature (and other climate variables) (Figure 2). Thus, one would expect the area of land occupied by Mount Rainier’s tree species (the *ranges* of these species) to shift upwards with warming.

This expectation of upward range shifts is supported by a study that reconstructed the last 6000 years of forest history at three sites at Mount Rainier by examining pollen and tree macrofossil samples deposited in pond sediments (Dunwiddie 1986). The study indicates that lower elevation species were more abundant during warmer periods while higher elevation species were more abundant during cooler periods, suggesting that the ranges of tree species at Mount Rainier are sensitive to changes in climate. In addition, recent decades have seen an increase in the background rates of tree mortality in Pacific Northwest forests, a trend thought to be caused by higher temperatures and greater drought stress (van Mantgem et al. 2009). This increased mortality has the potential to alter the structure, composition and productivity of Mount Rainier’s forests. However, there was little change in the structure and composition of mature forest stands between the mid-1970s and the mid-1990s, despite changes in climate (Acker et al. 2006). This is not surprising, though, given the long lifetimes of the tree species in the Park. Thus, climate change induced range shifts could be substantial but will likely be very slow in the absence of major disturbances. In addition, a study of how climate affects tree growth at Mount Rainier found that patterns in growth were well correlated with patterns in climate at the highest elevations (near treeline) but not lower elevations, where tree growth was apparently more strongly dictated by other factors (Ettinger et al. 2011). This could make responses of trees to climate change idiosyncratic and difficult to predict.

However, major disturbances do occur in the Park. Historically, fire has been the most important disturbance and around 90% of the Park’s forest has arisen after fire, with pre-European settlement fire return intervals of around 465 years (Franklin et al. 1988). Fire will probably become more frequent in the future due to higher summer temperatures and decreased summer precipitation creating drier conditions, making fire more likely. However, statistically based predictions of changes in fire regime cannot currently be made for forests in the western Cascade Mountains because of the long fire return intervals (Littell et al. 2009). But periods in the past with warmer temperatures were associated with a higher abundance of tree species that tend colonize recently burned areas, suggesting that fires at Mount Rainier were more prevalent during these periods (Dunwiddie 1986). Predicted changes in fire regime would likely alter forest structure, composition and productivity, accelerate tree species range shifts, and create threats to human lives and infrastructure (including buildings and roads that are part of the Mount Rainier National Historic Landmark District) (Littell et al. 2009).

Subalpine and alpine meadows

The subalpine and alpine meadows of Mount Rainier National Park form a diverse and ecologically important component of the Park's flora, and protecting these plant communities is important for maintaining biodiversity within the Park. For example, a majority of the Park's imperiled or rare plant species are found in subalpine or alpine environments. These meadows also provide important habitat for wildlife such as mountain goats, white-tailed ptarmigans, hoary marmots and the American pika (NPS 2001). In addition, the meadows are a popular destination in the Park, with about 65% of visitors travelling to the meadows to view wildflowers (NPS 2000).

Subalpine and alpine meadows are found at high elevations where temperatures are too cold or snow covers the ground for too long for trees to grow. They are found between about 1650m and 2000m on the west side of the Park, and 1900m and 2200m on the east side. At lower elevations, trees outcompete meadow species. At higher elevations, conditions are not suitable for any plants to cover a large fraction of the ground, and only a few plants are able to establish in sheltered “microhabitats.” Meadows are probably found at lower elevations on the west compared to the east side of the Park because the west receives more snowfall, which shortens the snow-free period of the year. Topographic features can also be important in determining the distribution of these meadows. For example, in the subalpine zone of the Park, meadows are typically found in depressions in the landscape (where large amounts of snow accumulate and snow-free periods are short), while patches of trees occupy ridges where relatively little snow accumulates and snow-free periods are longer.

These meadows are dynamic ecosystems. Trees, mostly subalpine fir, have readily invaded the subalpine meadows of the Park over the course of the 20th century in association with warmer temperatures (Franklin et al. 1971, Henderson 1974, Rochefort and Peterson 1996). These tree invasions have also been documented in a variety of other locations in the West (reviewed in Rochefort et al. 1994) and the rest of the world (reviewed in Harsch et al. 2009), though forest encroachment does not universally result when temperatures increase (Harsch et al. 2009). In addition, studies from Mount Rainier and other locations have shown that meadow plant species are able to colonize new habitat that was previously covered by ice or bare ground under favorable climatic conditions (Henderson 1974, Grabherr et al. 1994, Gottfried et al. 1999, Walther et al. 2005, Pauli et al. 2007, Cannone et al. 2008). Thus, increasing temperatures could cause the total geographic range of these meadows to shrink, expand or remain the same, depending on the relative rates at which meadow species colonize bare land and trees invade meadows.

However, a general upward movement of the meadows will likely reduce the area of land they occupy because there is less land at higher elevations due to the conical shape of mountains. And although meadows occupying the flanks of the volcano have high elevation land available to potentially colonize, meadows in the Park that occupy the peaks of lower elevation mountains will have no “escape route.” Furthermore, forests might move into meadows faster than meadows expand onto bare ground because the lack of well developed soil on bare ground could slow the establishment of meadow plants, while trees would not face this constraint while establishing in meadows. This difference in rates of establishment by trees and meadow plants could also lead to meadows shrinking.

The length of the snow-free period is thought to be the primary determinant of whether trees are able to establish in subalpine meadows or not, with longer snow-free periods favoring establishment (Franklin et al. 1971). Higher temperatures are predicted to lead to reductions in snow pack (Elsner et al. 2009) which would, in turn, likely lead to lengthened snow-free periods and higher rates of tree establishment. Warmer temperatures during the growing season also generally favor tree establishment (Rochefort et al. 1994), indicating that the higher temperatures predicted for the Pacific Northwest (Mote and Salathé 2009) will also directly increase the rate of tree invasion. However, trees also require adequate summer soil moisture to establish in subalpine meadows (Rochefort et al. 1994). In the Pacific Northwest, precipitation is expected to decrease in the summer (Mote and Salathé 2009), which, along with elevated temperature, would increase drought stress experienced by tree seedlings. This elevated drought stress would tend to lower rates of establishment.

Non-climatic factors also have the potential to help set the geographic range of these meadows. For instance, animal grazing has the ability to either enhance or detract from tree establishment, depending on the animal’s preference for tree or meadow forage, the impacts of trampling on the soil and the potential of the animals to disperse tree seeds into meadows (Cairns and Moen 2004). Fire also has the potential to expand the geographic distribution of subalpine meadows, at least on a small scale and for a period of decades. The ability of fire to create or maintain subalpine meadows has long been noted at Mount Rainier (Henderson 1974, Allen 1916, Griggs 1938, Stueve et al. 2009) as well as other locations (Kuramoto and Bliss 1970, Peet 1981, Shankman 1984). These studies have shown that high elevation trees are slow to reestablish after fires and that forests can often take several decades to regenerate. In the meantime, meadow vegetation predominates. Some of the past fires in the subalpine meadows of Mount Rainier were lightning ignited or accidently set by humans, but early reports state that other fires were intentionally lit by Yakama and Klickitat Native Americans to increase huckleberry production, make the landscape easier to traverse, create forage for their horses and improve deer hunting (Allen 1916, McIntyre 1952). Thus, some of the forest encroachment into subalpine meadows observed at Mount Rainier may be due to recovery of forest patches after fire disturbance, and not necessarily the response of an established ecological boundary to changes in climate.

The subalpine and alpine meadows of Mount Rainier are dynamic ecosystems and there are many factors that determine their geographic ranges. However, large increases in temperature and corresponding decreases in snowpack will, in all likelihood, lead to upward movement of the meadows and a reduction in the area of land they occupy. The reduction in area occupied by the meadows could lead to a loss of some of the meadow species from the Park.

Species at risk

Virtually all of the species Mount Rainier supports will be affected by climate change in some way. Many of these species will likely be at risk of decline within the Park and throughout their range. In this section, I discuss in detail two species that could be in jeopardy: whitebark pine and the American pika. These case studies exemplify the risks species face and the complexities of predicting species responses to climate change. However, other species have been identified as being vulnerable to climate change while others still are likely to be vulnerable but have received little scientific attention. Thus, climate change will likely have profound effects on the biological communities of the Park.

Whitebark pine

The whitebark pine (scientific name: *Pinus albicaulis*) is an important tree species at Mount Rainier and in many mountainous regions of western North America because of its role in shaping habitat and providing food (in the form of its large seeds) for a variety of animals. The species is considered to be imperiled by climate change and other factors. Although far from being the only plant species at risk because of climate change, the whitebark pine has received a lot of focus because of its important role in many mountain ecosystems and provides a good example of how climate change and other human-caused factors will affect plant species.

Background and non-climate change threats to the whitebark pine

The whitebark pine is prevalent at Mount Rainier and in many mountainous areas in western North America. It is most abundant at dry, high elevation sites and is typically found on the north and east sides of the Park at elevations above about 1500m (or about 5000ft) (Biek 2000). There are approximately 22,000 adult whitebark pines found throughout the Park (Cottone and Ettl 2001).

Whitebark pine is considered a "foundation species" in certain subalpine ecosystems because the large, nutrient rich seeds it produces are an important food resource for a number of animal species (Ellison et al. 2005). Unlike most pines, which have seeds that are carried away from the parent tree by the wind, whitebark pine seeds lack wings and primarily rely on a mutualistic relationship with a bird called the Clark's nutcracker for dispersal (Tomback et al. 2001). The cones of the whitebark pine generally remain closed until pried open by the beak of a Clark's nutcracker which eats the seeds or stores them in a pouch under its tongue for transport. Clark's nutcrackers can hold over 150 whitebark pine seeds in this pouch at a time. The bird then caches these seeds for later consumption, but typically caches far more seeds than it can eat. The forgone seeds can then germinate and grow into an adult tree. Clark's nutcrackers often cache these seeds at the sites of recent burns, allowing the whitebark pine to be one of the first trees to colonize these disturbed sites. The caches are also an important food source for a variety of animals, including bears and a number of small mammals (Tomback et al. 2001).

The whitebark pine currently faces a number of serious threats. One is a non-native fungal disease introduced to North America in 1910 called the white pine blister rust (Tomback et al. 2001). The blister rust soon spread throughout most of the range of the whitebark pine. The pathogen was first discovered in Mount Rainier in 1928 on western white pines and was observed on whitebark pines in 1937 (Rochefort 2008). In a survey conducted in the Park from 1994-1999, Rochefort observed that 13.5% of whitebark pine trees were infected with the blister rust and 33.4% were dead (presumably, but not necessarily, from the blister rust), while 24.3% of whitebark pine saplings were infected and 8.6% were dead (2008). Given these high mortality rates and the tree's slow growth, the long-term persistence of the whitebark pine at Mount Rainier is in question. Ettl and Cottone developed a model of whitebark pine populations at Mount Rainier that predicts there will be less than 100 whitebark pine trees in the Park in 148 years given current demographic trends (2004) (Figure 3).

In addition, fire suppression may also be contributing to the decline of whitebark pine at Mount Rainier. Whitebark pine tends to thrive in post-fire environments, but is often outcompeted by other species, such as subalpine fir, in the absence of disturbance (Tomback et al. 2001). However, a study of historical fire regimes at whitebark pine stands in the Park shows a high degree of variability across the Park in terms of fire frequency (Siderius and Murray 2005). For instance, there was little to no evidence of fire at whitebark pine stands near the volcano itself, suggesting that fire has not been responsible for maintaining these stands in the past. But there was evidence of frequent fires (~50 year return intervals) at the stands around Crystal and Deadwood Lakes along the eastern border of the Park, with a wide range of severities. Fire may have played a significant role in sustaining whitebark pine populations at these locations.

Climate change threats to the whitebark pine

Climate change creates yet more potential threats to the whitebark pines at Mount Rainier. One of these threats is a potential increase in the likelihood and severity of mountain pine beetle (MPB) outbreaks. The MPB is an insect native to North America that bores into pine trees to lay eggs under the tree's bark. When the eggs hatch, the emerging larvae consume the tree's vascular tissue, and if the infestation rate is high enough the beetles can girdle and kill the trees (Gibson et al. 2008). Currently an unprecedented outbreak of the MPB is occurring in British Columbia that has destroyed over 130,000 square kilometers of lodgepole pine forest, an area four times the size of Vancouver Island (Ministry of Forests, Lands and Natural Resource Operations 2008).

The high elevation habitats of whitebark pines have historically been too cold to allow MPB populations to reach epidemic proportions in most years (Logan and Powell 2001). However, outbreaks have occurred in whitebark pine stands in the past in conjunction with above average temperatures (Gibson et al. 2008). Higher temperatures are believed to enable MPB epidemics because they increase the beetle’s survival rate and allow the insect to complete its life cycle in one year (as opposed to the typical two at high elevations) (Logan and Powell 2001), leading to large populations that can synchronously attack trees and override their defensive mechanisms (Amman et al. 1997). Climate change is expected to increase the likelihood of high elevation whitebark pine stands experiencing the warm temperatures amenable to MPB outbreaks (Logan and Powell 2001). Consistent with this expectation is the observation in recent years that the MPB has expanded its range to higher elevations in association with increasing temperatures (Gibson et al. 2008).

However, at Mount Rainier the MPB has only rarely been observed in whitebark pine stands and is not believed to be a major cause of mortality (Rochefort 2008). The lack of infestation could be due in part to the absence of large stands of lodgepole pines in Mount Rainier (Rochefort 2008). In areas with abundant lodgepole pine populations, outbreaks in stands of these lower elevation trees can often “spill over” into higher elevation whitebark pine stands, causing widespread whitebark pine mortality (Tomback et al. 2001). However, whitebark pine stands can sustain MPB outbreaks even in the absence of neighboring lodgepole pine stands, if the climate is suitable (Logan and Powell 2001). Thus, the MPB could become a serious threat to whitebark pine stands at Mount Rainier as temperatures continue to rise (Rochefort 2008).

Climate change may also affect the severity of white pine blister rust infestations in whitebark pine stands. Mortality from the blister rust declines with increasing elevation in the Park, potentially because the shorter growing season at higher elevations reduces the rate at which the pathogen can spread in the tree (Rochefort 2008). If climate change prolongs the growing season, whitebark pines could experience increased mortality from the blister rust (Rochefort 2008).

It is also important to note that these multiple stressors will not act alone, but instead will likely interact synergistically to threaten whitebark pine populations. For example, whitebark pines weakened by white pine blister rust and suffering from competition with trees that have established in the absence of fire will be more likely to succumb to MPB infestations (Ellison et al. 2005, Tomback et al. 2001). Due to this litany of threats, the International Union for Conservation of Nature has listed the whitebark pine as “vulnerable” on its Red List of Threatened Species (Reuling 2008) while the Natural Resource Defense Council has petitioned for the species to be listed as endangered under the Endangered Species Act (NRDC 2008). The US Fish and Wildlife Service reviewed the status of the whitebark pine and determined that listing the species is warranted. However, the US Fish and Wildlife Service cannot currently place whitebark pine on the endangered or threatened species lists because of higher priority actions (US Fish and Wildlife Service 2011).

It is also possible that whitebark pines could be favored, to some extent, by the potential increase in fire frequency due to climate change because fires create good opportunities for whitebark pine establishment. However, the benefits of increased establishment could be outweighed by the costs of tree mortality if the disturbances tend to be high intensity stand-replacing crown fires as opposed to low intensity surface fires.

Even in the absence of climate change, the whitebark pine would face several threats to its existence. Future climate change will likely exacerbate these other threats and create new ones, making the long-term persistence of this already imperiled species even less certain.

The American pika

The American pika (scientific name: *Ochotona princeps*) is a small mammal that lives at high elevations at Mount Rainier National Park and in cold environments at many locations in western North America from the southwestern United States to British Columbia and Alberta in Canada. The species could face serious threats from a changing climate. Though far from the only wildlife species to be threatened by climate change, the vulnerability of the pika to warming has been the focus of several recent studies and legal actions. Thus, the pika provides a useful case study for how animal species in mountainous habitats such as at Mount Rainier may respond to climate change.

Pikas are solitary and territorial animals that maintain dens in piles of boulders and rocks, and forage in the surrounding vegetation (typically alpine and subalpine meadows). During the summer, pikas directly consume plants in the meadows, but also bring some of this vegetation back to their dens to create stockpiles of food called haypiles (Smith and Weston 1990). The pika has been considered a “keystone species” in high elevation meadows because its grazing appears to have a large effect on the species composition of these plant communities, particularly in its ability to enhance the persistence of cushion plants (Huntly 1987, Power et al. 1996). These animals remain in the same high elevation territories year round (Smith and Weston 1990). They do not hibernate in the winter and must feed on surrounding vegetation (which they can access via snow tunnels) or on haypiles in their dens (that they build up during the summer) to survive (Smith and Weston 1990). In fact, pikas have been known to cache plants with high levels of toxins, wait until late in the winter when these toxins have degraded and then consume the now palatable plants. In the meantime, the toxins have slowed plant decomposition and helped provide a long-lasting food supply for the pika. In this way, the pikas have apparently co-opted the plant toxins (presumably an anti-herbivore defense) for food preservation (Dearing 1997).

Climate change could pose serious threats to the pika. These mammals have very low heat tolerance and exposure to temperatures between 26ºC and 29ºC (79ºF and 84ºF) for several hours can be lethal (Smith 1974a, MacArthur and Wang 1973). Given this low tolerance, higher summer temperatures could result in portions of the pika’s current range becoming uninhabitable as lethal temperatures become more common (Beever et al. 2003). High temperatures have also been correlated with altered activity levels that force pikas to forego their typical midday foraging (Smith 1974a). Elevated summer temperatures brought about by climate change could reduce the amount time pikas can forage during the day, potentially preventing them from gaining sufficient biomass or collecting sufficient hay to survive the winter (Beever et al. 2003). The reduced foraging opportunities could be especially harmful to pikas given their high metabolic rate (pikas must fill their stomachs nine times a day to meet their energy demands) (Smith and Weston 1990).

It seems likely that higher temperatures would force pikas upward in elevation and northward in latitude. The results of a study in Yosemite National Park supported this expectation by documenting a 153 meter increase in the lower elevational limit of the pika since the early 20th century, in association with rising temperatures (Moritz et al. 2008). Similarly, Grayson 2005 estimated that the average elevation of pikas in the Great Basin region of the Southwestern US has increased by 152 meters in recent times (2005). This trend will likely decrease the amount of habitat available to pikas, since there is less land at higher elevations or no land at all if pika populations already occupy a summit. In addition, pikas would likely have difficulty moving northward from one mountain peak to another due to their limited dispersal ability – maximum dispersal distances are typically 3 kilometers (Smith 1974b) and dispersal across warm, low elevation lands are particularly unlikely (Smith 1974a). Perhaps a testament to their limited dispersal abilities, pikas are not found in the Olympic Mountains despite being common in the nearby Cascade Mountains, presumably because they have not been able to cross the warm, unsuitable Puget Sound lowlands which separate these two mountain ranges.

Results from a series of studies of pika populations in the Great Basin are consistent with the expectation that pikas will be vulnerable to climate change. Beever et al. 2011 have re-surveyed 25 sites in the Great Basin where pika populations had been observed at some point during the 20th century and found that ten have apparently been extirpated (died out), including four since 1999 (2011). Extirpated sites tended to be at low elevations (relative to latitude) and to have high summer temperatures compared to surviving populations (Beever et al. 2003, Beever et al. 2011, Beever et al. 2010, Wilkening et al. 2011), suggesting that pikas are sensitive to high temperatures and that documented warming trends might have played a role in these extirpations.

However, summer temperature is probably not the only factor governing pika extirpations in the Great Basin. Extirpated sites tended to experience more days during the winter with extremely low temperatures (less than -10°C or 14°F) within the rock piles where pikas make their dens (Beever et al. 2011, Beever et al. 2010). Sites likely experienced these extremely low temperatures because of a lack of snow cover that can insulate the rock piles and maintain temperatures around the freezing point, a relatively high temperature during winter in these high elevation environments. These extremely low temperatures are likely stressful for pikas and could increase mortality. Livestock grazing and being outside of designated wilderness areas were also correlated with pika extirpations, indicating that climate is not the only factor important in determining the persistence of pika populations. In fact, a new population of pikas was recently discovered in the Great Basin at a low elevation, high temperature site, showing that there is not a strict relationship between pikas and climate (Beever et al. 2008).

But in spite of these complicating factors, one of the main messages to come out of this research is that pikas are sensitive to warming and appear to be declining in the Great Basin. Furthermore, these trends might be representative of the threats the species faces throughout its range. This view is bolstered by a study in which (Galbreath et al. 2009) created computer models of the climate pikas tend to occur in (the pika's *climate envelope*) and found that the area of land in western North America that experiences this climate will likely shrink dramatically given projections of warming for the 21st century. Presumably, this reduction in the pika's climate envelope will lead to a reduction in pika population size. These concerns for pika populations led the Center for Biological Diversity (CBD) to petition to have the species listed as "threatened" under the US Endangered Species Act (CBD 2007).

However, there are several lines of evidence that suggest the species as a whole may be well suited to cope with climate change. For example, Millar and Westfall recently surveyed a large number of sites in the Sierra Nevada Mountains, as well as parts of the Great Basin and Oregon Cascade Mountains, and found a large number of pika populations, suggesting that the species is currently abundant in this region (2010). In addition, they found that pikas currently occur in a wide range of elevations and experience a wide range of temperatures. However, the authors did find that sites with suitable pika habitat (i.e. large rock piles) but without pikas were substantially warmer than sites currently occupied by pikas. Together, these data suggest that although climate change could make some current pika habitat too warm for pikas to persist, it is unlikely that it could make all currently occupied sites too warm for the species. Pikas have also been known to adjust their behavior to cope with high temperatures by resting inside shady rock piles during hot weather (MacArthur and Wang 1974) and shifting their foraging to cooler times of day, and have even been observed foraging at night when daytime temperatures are high (Smith 1974a). This behavioral flexibility could aid the pika in surviving a warmer world.

Citing the lack of evidence that the species as a whole, or any of its five subspecies, will likely be driven to extinction by climate change (at least in the "foreseeable future") the US Fish and Wildlife service found that protection of the pika under the Endangered Species Act is not currently warranted (US Fish and Wildlife Service 2010). However, this does not mean the pika is free from danger. Certain populations may still be extirpated by climate change, and the status of the species beyond the foreseeable future (which the US Fish and Wildlife Service defined as being the middle of the 21st century) is uncertain. Thus, unmitigated climate change could still very well pose a threat to the pika.

Given the challenges faced by the pika in this period of rapid climate change, Mount Rainier will likely become an increasingly important refuge for the species. The non-climate stressors experienced by pikas (livestock grazing and recreational hunting) are not present in the Park (Beever et al. 2003, Beever et al. 2011). In addition, Mount Rainier has an abundance of rock piles and boulder fields at high elevations, which serve as important, cool shelters for pikas that will likely be critical for surviving a warmer climate (Beever et al. 2011, Millar and Westfall 2010). Thus, if pikas populations do rapidly decline because of climate change in the region, Mount Rainier would likely be one of the best remaining habitats for the species and could become increasingly important for the species' survival. In fact, Mount Rainier's abundance of high elevation lands and protected wilderness will likely make the Park an important refuge for many of the region's mountain-dwelling species in a warming world.

Other species potentially at risk

There are several other species present at Mount Rainier National Park that are thought to be at risk due to climate change that I would like to briefly discuss. One is the bull trout, a “threatened” species under the Endangered Species Act that depends on cold water for spawning and early rearing. Climate is thought to strongly limit the geographic distribution of this fish, and climate change is expected to result in a large loss of habitable area (Rieman et al. 2007). The “threatened” Puget Sound population of Chinook salmon, which are thought to occur in the Park in small numbers (NPS 2001), could also be harmed by changes in stream temperature and increased flooding that are predicted to accompany climate change (Mantua et al. 2009). In addition, it has been speculated that other alpine animals, besides the American pika (discussed above), will be sensitive to climate change because of the possible reduction and fragmentation of alpine habitat. These species include the mountain goat, white-tailed ptarmigan and hoary marmot (Martin 2001). And there are still other species in the Park which have been identified as potentially vulnerable to climate change, but have not been discussed here. Furthermore, species not known to be seriously at risk could in fact be threatened by climate change for currently unidentified reasons. Climate plays an important role in the life history of virtually every species, so an exhaustive list of species that will be positively or negatively affected by climate change is probably impossible to create.

Conclusions

Climate change will likely create or exacerbate a variety of problems for conserving the resources and values of Mount Rainier National Park. A number of these problems will probably be unprecedented in the history of the Park. Many of the geological, biological, cultural and historical features that the Park was created to protect will be at risk of degradation or elimination. Preservation of these resources will require a combination of global scale actions to reduce greenhouse gas emissions and local efforts in the Park to adapt to the changes likely to take place this century. However, climate change will pose these threats to natural resources everywhere. In general, these resources will probably be best preserved within protected areas such as Mount Rainier where there are fewer direct threats from human activity (i.e. habitat destruction). The high elevation habitats of the Park will also sustain relatively cool climates that will become progressively more rare in the lower elevation landscapes surrounding the volcano, making Mount Rainier an increasingly important refuge for cold-adapted species. In an age of rapid warming, Mount Rainier is more important than ever for preserving the region's natural resources and biodiversity.

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Figures

Figure 1. The Nisqually Glacier, situated on the South side of Mount Rainier, has receded over the last century and exposed a large amount of unstable soil. Destructive debris flows have originated from these recently exposed areas (photo credit: wikimedia.org).

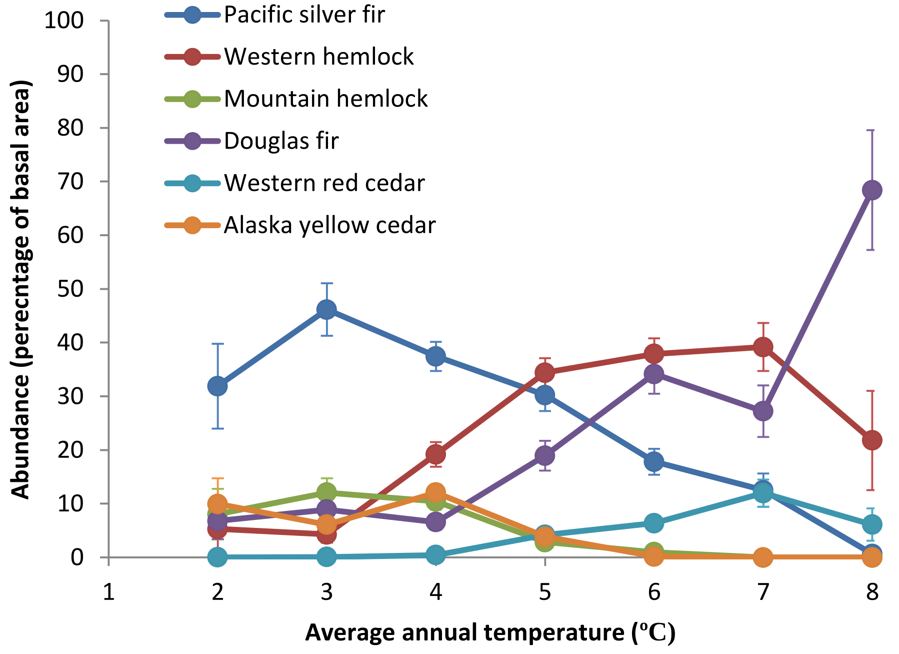

Figure 2. The relationship between tree species abundance and average annual temperature. Tree abundance is measured in terms of the percentage of total tree basal area for the given species (basal area is the area of a cross section of a tree's trunk measured at 137cm, or 4.5ft, above the ground). Error bars show standard error. The temperature data was produced by the PRISM climate model (Daly et al. 2008), while the data on tree abundance came from surveys of forest plots around the Park (Franklin et al. 1988).

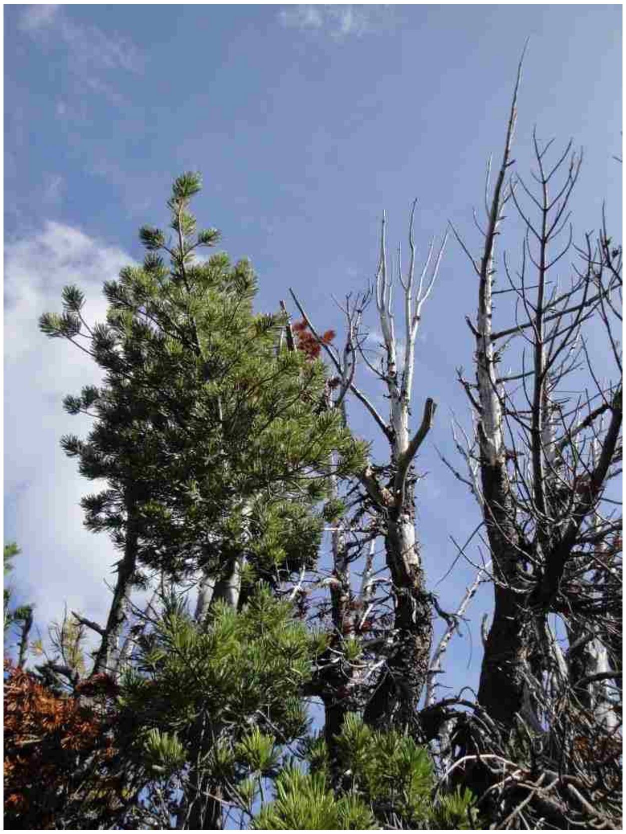

Figure 3. Patch of live and dead whitebark pines near Sunrise.

Chapter 2: Spatial heterogeneity in ecologically important climate variables at coarse and fine scales in a high-snow mountain landscape

Kevin R. Ford, Ailene K. Ettinger, Jessica D. Lundquist, Mark S. Raleigh, Janneke Hille Ris Lambers

Abstract

Climate plays an important role in determining the geographic ranges of species. With rapid climate change expected in the coming decades, ecologists have predicted that species ranges will shift large distances in elevation and latitude. However, most range shift assessments are based on coarse-scale climate models that ignore fine-scale heterogeneity and could fail to capture important range shift dynamics. Moreover, if climate varies dramatically over short distances, some populations of certain species may only need to migrate tens of meters between microhabitats to track their climate as opposed to hundreds of meters upward or hundreds of kilometers poleward. To address these issues, we measured climate variables that are likely important determinants of plant species distributions and abundances (snow disappearance date and soil temperature) at coarse and fine scales at Mount Rainier National Park in Washington State, USA. Coarse-scale differences across the landscape such as large changes in elevation had expected effects on climatic variables, with later snow disappearance dates and lower temperatures at higher elevations. However, locations separated by small distances (~20 m), but differing by vegetation structure or topographic position, often experienced differences in snow disappearance date and soil temperature as great as locations separated by large distances (>1 km). Tree canopy gaps and topographic depressions experienced later snow disappearance dates than corresponding locations under intact canopy and on ridges. Additionally, locations under

vegetation and on topographic ridges experienced lower maximum and higher minimum soil temperatures. The large differences in climate we observed over small distances will likely lead to complex range shift dynamics and could buffer species from the negative effects of climate change.

Introduction

Biologists have long recognized the fundamental role climate plays in determining the geographic distributions of species and biomes (Humboldt and Bonpland 1807, Merriam and Steineger 1890, Whittaker 1975). As a result, climate change is expected to induce shifts in the geographic ranges of species. This prediction is supported by the many observations of upward or poleward range shifts over the last 100 years consistent with observed warming (Chen et al. 2011) as well as range shifts inferred from the fossil record (Davis and Shaw 2001, Lovejoy and Hannah 2005). Alarmingly, models of the impacts of future anthropogenic climate change on species ranges have forecasted widespread extinction risks as the climatic niche of many species disappears or shifts faster than species can likely migrate (Fischlin et al. 2007, Loarie et al. 2009).

However, these projections of climate change-induced range shifts (and subsequent extinction risks) are sensitive to the spatial scale at which the analyses are conducted (Levin 1992). Most range shift assessments rely on gridded maps of climate variables with grid cell sizes ranging from 800x800 m (e.g. PRISM – Daly et al. 2008 and WorldClim – Hijmans et al. 2005) up to 50x50 km (e.g. Thuiller et al. 2005). The finer scale maps (800x800 m grid cells) capture a wide variety of climatic patterns, but the scales of these maps are still far coarser than the scales at which organisms experience their environment. Thus, these climate maps may hide fine-scale differences in climate that are important for organism distributions (Guisan and Zimmermann 2000). For example, north and south facing slopes separated by tens of meters may receive different amounts of solar radiation and experience very different temperature regimes (Geiger et al. 2009, Ackerly et al. 2010), which could lead to differences in species composition within these microhabitats.

The implication of significant fine-scale climatic heterogeneity that is not captured by coarse-scale climate maps is that projections based on these maps could fail to capture important range shift dynamics. For example, cool microhabitats (such as north-facing slopes in the Northern Hemisphere) near the contracting edge or core of a species' distribution may allow populations of that species to persist if individuals can disperse to them from warmer microhabitats (such as south-facing slopes in the Northern Hemisphere), even if most of the surrounding landscape becomes unsuitably warm (as long as these microhabitat types comprise a total area large enough to support a population – Tamme et al. 2010). At the same time, warm microhabitats beyond the advancing edge of a species' range may provide the first sites of colonization that allow that species to migrate to new locations. Thus, instead of needing to move hundreds of meters upward or hundreds of kilometers poleward to track suitable climate, many species may only need to move tens of meters from one microhabitat to another and could be buffered from the negative effects of climate change (Willis and Bhagwat 2009).

For such fine-scale climatic heterogeneity to strongly influence range dynamics, however, fine-scale differences in climate must be large relative to coarse-scale differences. We addressed this issue by examining the magnitude of fine-scale heterogeneity relative to coarse-scale heterogeneity in snow disappearance date and growing season soil temperature. Specifically, we deployed 284 microclimate sensors across a ~1500 m elevation gradient spanning forest, subalpine and alpine biomes at Mount Rainier National Park. Our objectives were to 1) quantify snow disappearance date and soil temperature as a function of coarse-scale differences in elevation and exposure to storm tracks (i.e. being on the windward or leeward side of the mountain) and fine-scale differences in vegetation structure or topography, 2) compare fine-scale differences in climatic variables (that would be missed by climate models) to coarse-scale differences (that would be captured by climate models), and 3) determine whether fine-scale patterns in climatic variables related to topography (but not vegetation structure) are correlated with fine-scale patterns in vegetation characteristics. We focus on snow disappearance date and growing season soil temperature because snow disappearance date influences the length of the growing season (especially important in this region where the growing season can be very short due to the persistence of large winter snowpacks) while soil temperature strongly influences plant growth rates and other physiological processes (Larcher 2003). These variables have also been shown to be strongly associated with patterns of distribution, abundance, productivity and diversity of plant species, at our sites and others (Franklin et al. 1988, Wipf and Rixen 2010, Scherrer and Körner 2011). Additionally, both variables are likely to change in the coming decades as a result of anthropogenic climate change, with rising temperatures and declining snowpacks leading to warmer and longer growing seasons (Mote and Salathe 2010, Elsner et al. 2010).

It has long been known that climate can vary dramatically at fine spatial scales (reviewed in Geiger et al. 2009 and Clark et al. 2011), but these patterns have only recently begun to be studied explicitly and systematically with respect to the impacts of climate change on species distributions. Studies have found that locations separated by only tens of meters experienced mean seasonal soil temperatures that differed by 3-7°C, equivalent to the average temperature difference experienced in locations separated by hundreds of meters in elevation or hundreds of kilometers in latitude (Ackerly et al. 2010, Scherrer and Körner 2011, Fridley 2009, Millar and Westfall 2010, Scherrer and Körner 2010, Wundram et al. 2010). Moreover, such large differences in temperature are known to strongly influence organismal performance (Larcher 2003, Deutsch et al. 2008) and are greater than the expected increase in temperature due to climate change in many parts of the globe (Meehl et al. 2007). Similarly large differences were also observed in air temperature, snow cover duration or snow disappearance date over fine spatial scales in these studies. Our paper builds on these case studies and is notable for its large sample size of 284 sensors (important for assessing microclimate patterns in a statistically rigorous way), its explicit comparison of coarse- and fine-scale climatic heterogeneity (important for assessing the biases of coarse-scale models) and the broad environmental gradients covered (important for assessing how widespread these biases may be).

Methods

Study area

Mount Rainier National Park encompasses 95,354 ha of land in the western Cascade Mountains in Washington State, USA (Figure 1). The region experiences a temperate, maritime climate with mild, dry summers and cool, wet winters that produce large snowpacks. Elevation ranges from 518 m in the deep valley floors to 4392 m at the peak of Mount Rainier, the volcano located in the middle of the Park. The mountainous terrain produces steep climatic gradients: temperature decreases and precipitation increases with elevation, while the rainshadow effect produced by the volcano leads to lower precipitation on the east side of the Park. There are two primary climate stations in the Park. At the station located at 842 m elevation, mean annual temperature is 6.6ºC and mean annual precipitation is 2030 mm; at the 1654 m station, mean annual temperature is 3.7ºC and mean annual precipitation is 3005 mm (1981-2010 normals, NOAA National Climate Data Center – www.wrcc.dri.edu/Climsum.html).

The large climatic gradients create three major biomes in the Park. The forest biome extends from the lowest elevations of the Park up to about 1600-2000 m and is dominated by coniferous trees. The subalpine biome typically extends about 300 m above the upper limit of the forest and is a mosaic of conifer tree patches and subalpine meadows. The alpine biome occupies the highest elevations, stretching from 1900-2300 m to the summit of Mount Rainier, and consists of large patches of mostly continuous alpine meadows (dominated by forbs, grasses and dwarf shrubs) near the lower limit of the biome, with exposed rock, glaciers, bare soil, and cryptogams (mostly mosses, lichens, algae and cryptobiotic soil crusts) predominating above.

Study design

From September 2009 through October 2010, we deployed 284 soil temperature sensors (HOBO Pendants made by the Onset Computer Corporation and iButtons made by Maxim Integrated Products) across Mount Rainier at elevations ranging from 638 m to 2164 m as part of two different plant ecology studies where microclimate was measured as an explanatory variable. The first study took place in the forest biome and spanned the elevational range of forests on the south side of Mount Rainier. The second study took place in the subalpine and alpine biomes, with study sites set up at the lower limit of the subalpine biome and the upper limit of alpine meadows on three sides of the mountain (Figure 1). Microclimate data from these studies were ideally suited for our questions as they covered large elevational gradients with sensors at each location stratified by vegetation or topographic features expected to influence microclimate. Due to differences in study design (described below), we analyzed the microclimate data from the two studies separately. The sensors remained in place and logged data until we collected them in September/October 2010.

For each sensor, we calculated the values of four climatic variables: snow disappearance date, and average daily mean, maximum and minimum soil temperature. We could assess snow cover from soil temperature measurements because snow insulates soil from fluctuations in air temperature so that temperatures beneath the snowpack in this region remain constant around 0ºC. Thus, the soil temperature data allowed us to determine whether snow was covering the sensor for each day the sensor was deployed using an algorithm that considers daily temperature ranges and maxima (Lundquist and Lott 2008, Raleigh et al. 2013). We calculated average daily mean, maximum and minimum soil temperature for periods in Summer/Fall 2010 when all sensors in a study experienced snow-free conditions and reported data. This period was August 14 through October 3, 2010 for the sensors in the forest study and August 11 through August 18, 2010 for the sensors in the subalpine/alpine study. This meant we only used a portion of the snow-free temperature data for some sensors, even though temperatures outside this period are likely to also be ecologically relevant. However, it was necessary to use the same time period for all sensors in a study so that temporal differences in the snow-free period between locations did not confound our analysis of spatial differences in temperature.

Arrays of sensors were deployed at 13 sites throughout the Park. For the forest study, we established three study sites along an elevation gradient in Summer 2009, allowing us to calculate snow disappearance date in 2010. We quantified growing season soil temperature in Summer/Fall 2010 at these three sites plus an additional four sites along the same elevation gradient. Within each site, we deployed sensors under gaps in the forest canopy caused by tree falls (“gaps”) and in locations under intact canopy within 20 m of one of the gaps (“non-gaps”). Each study site contained five of these gap/non-gap pairs. Gaps were ~130 m^2 on average. Within each gap or non-gap location, we placed one sensor in a 5.5x1.5 m area where all understory vegetation up to 2 m tall had been experimentally removed since early Summer 2009 (the “removed” plot) and one sensor at an adjacent location 2 m away where the vegetation had been left undisturbed (the “control” plot) (Figure 2A, Table 1).

For the subalpine/alpine study, we quantified microclimate at study sites on three sides of the mountain (south, northwest and northeast) which have different exposures to storm tracks and experience different precipitation regimes. On each side, we established two study sites, one close to the lower limit of the subalpine biome and one close to the upper limit of continuous alpine meadows, (below this limit, the ground is mostly vegetated while above it is almost entirely rock, glaciers and bare soil). These sites were about 200-300 m apart in elevation on each side of the mountain. Within each site, we established six linear transects that ran from a depression in the landscape up to a ridge (transects parallel to the slope) and were about 20 m in length. Within each transect, two sensors were located in the depression and two sensors were located on the ridge (Figure 2B, Table 1).

At each of the sensors in the subalpine/alpine biomes (where fine-scale sensor placement was stratified by topographic position and not vegetation structure), we measured vegetation characteristics in order to compare patterns in microclimate to ecological patterns. At the study sites near the lower limit of the subalpine biome, where closed-canopy forests transition to open meadows with increasing elevation, we measured percent cover by tree canopy above each sensor using a spherical densiometer (a gridded, hemisphere-shaped mirror used to estimate percent cover by foliage above a point on the ground), allowing us to assess the density of trees (higher values of tree canopy cover implies more or bigger trees). At the study sites near the upper limit of alpine meadows, where meadows transition to bare ground with increasing elevation, we estimated the percent of ground covered by vegetation at each sensor using a square-shaped PVC frame (1x1 m) placed on the ground adjacent to the sensor. String tied to the PVC frame created 100 evenly spaced grid points, allowing us to count the number of grid points overlaying vegetation in the area within the frame.

Data analysis

We used linear mixed effects models (LMMs) to characterize the relationships between the potential drivers of climate and each of the four climatic response variables (Zuur et al. 2009). The LMMs allowed us to estimate the effects of explanatory variables and their two-way interactions on the response variable (“fixed effects”) while statistically controlling for the effects of randomly selected experimental units on the response variable (“random effects”). At the forest sites, the drivers of climate were elevation, canopy structure (gap vs. non-gap) and understory structure (removed vs. control treatments), with gap/non-gap pair designated as a random effect. At the subalpine/alpine sites, the drivers of climate were side of the mountain (south vs. northwest vs. northeast), elevation (upper limit of alpine meadows vs. lower limit of the subalpine biome, treated as a categorical variable since there were only two values of elevation on each side of the mountain) and topographic position (depression vs. ridge), with sensor transect designated as a random effect. We verified that the residuals of these models were normally distributed, to validate our use of linear mixed effects models (rather than generalized linear mixed effects models).

For each model, we used Akaike’s information criterion (AIC) to select the most parsimonious combination of fixed and random effects to derive the “best-fit” model. Specifically, we used a three-step process following Zuur et al. (2009) where we (1) used AIC to determine the optimal random effects structure, selecting amongst several LMMs (fit with restricted maximum likelihood) that had different random effect terms (no random effects, random intercepts, random slopes or both), but the same fixed effect terms (which included all main effect and two-way interaction terms for each explanatory variable); (2) determined the optimal combination of fixed effect terms by using AIC to select amongst models (fit with maximum likelihood) with all possible combinations of fixed effect terms (but sharing the optimal random effects structure selected in the first step); and (3) fit a model with the random effects structure selected in the first step (which could be no random effects) and the fixed effects structure selected in the second step and considered this model to be our final "best-fit" model. This final model was fit with restricted maximum likelihood if it included random effects or maximum likelihood if it did not. All models were fit in R version 2.12.0 using the lme4 package for the LMMs (R Development Core Team 2010, Bates et al. 2011). See Appendix A for more details of the model fitting and selection procedure.

We assessed the significance of the model coefficients using Markov chain Monte Carlo sampling implemented with the MCMCglmm package in R (Hadfield 2010) or *t*-tests (when no random effects were included in the best-fit model). We then used the explanatory variable coefficients of the best-fit models to calculate the magnitude of differences in microclimate response variables relative to differences in the explanatory variables. For example, if the coefficients related to topographic position in the model of snow disappearance date at the subalpine/alpine sites indicated that the difference between ridges and depressions was 20 days, controlling for differences in other variables, then the effect of topographic position on snow disappearance date would be equal to 20 days. In order to compare the effects of elevation (which we consider a coarse-scale driver of climate) to the effects of other explanatory variables, we calculated the difference in snow disappearance date or temperature between two points 100 m apart in elevation for each model (controlling for differences in other variables). Like differences in climate amongst different sides of the mountain, differences in climate caused by a 100 m difference in elevation can typically be captured by coarse-scale climate models (e.g. PRISM), while differences caused by vegetation structure and fine-scale topography cannot. If one of the explanatory variables was not included in the best-fit model, we included the main effect of that variable in the final model for comparative purposes. This happened for one explanatory variable in one model (the understory structure variable in the snow disappearance date model in the forest study).

For sites in the subalpine/alpine biomes, we also fit linear models (LMs) to characterize the relationships between each of the four microclimate variables and percent cover by tree canopy at the lower elevation sites, and the relationships between each of the four microclimate variables and percent cover by ground vegetation at the higher elevation sites, for a total of eight LMs. In these models, the response variable was the vegetation characteristic while the explanatory variables were the microclimate variable, side of the mountain (included as a covariate) and their interaction. Using LMMs with sensor transect designated as a random effect did not improve model fit for any of the relationships, so we used the simpler LMs for all of these analyses. Next, we used AIC to select the best-fit LM. With one exception, this best-fit model included both the microclimate variable and side of the mountain, but not their interaction, as explanatory variables. In these cases, we used *t*-tests to assess the significance of the microclimate variable coefficient in the best-fit model in order to assess the significance of that microclimate variable. When modeling percent tree canopy cover at the lower elevation sites as a function of average daily minimum temperature and side of the mountain, neither explanatory variable nor their interaction was included in the best-fit model (i.e. the best-fit model was the null model with only an intercept). For this situation, we performed a *t*-test on the minimum temperature coefficient in a model that included both minimum temperature and side of the mountain, but not their interaction, as explanatory variables (i.e. a model with the same structure as the best-fit model for all the other vegetation-climate analyses) in order to assess the significance of minimum temperature.

We calculated the proportion of variance in the response variable explained by variance in the fixed effect explanatory variables (r^2) for all models, following Xu (2003).

Results

Variations in climate were explained by both coarse- and fine-scale drivers, with best-fit models having r^2 values ranging between 0.20 and 0.94 (Table 2). As expected, higher elevations experienced later snow disappearance dates and lower average daily mean and minimum temperatures (Figure 3A, B, D). However, the relationship between elevation and average daily maximum temperature was weak, and variability in this parameter was dominated by variability amongst locations at similar elevations (Figure 3C). At the subalpine/alpine sites, snow disappearance date and temperature varied depending on what side of the mountain sensors were on – e.g. the south side experienced later snow disappearance dates on average, probably because this side of the mountain is the most exposed to winter storms and receives the largest amount of winter precipitation. However, there were also substantial differences amongst locations at similar elevations for each of these variables that could be attributed to vegetation structure or topographic position (Figures 3, 4). We also assessed heterogeneity in growing degree days (GDD – calculated as the sum of daily mean soil temperatures for all days where the daily mean soil temperature was over 5°C), which showed patterns very similar to those of snow disappearance date (results not shown due to limitations of the data – sensors were not deployed long enough to estimate GDD for the full year or growing season, which could bias comparisons of GDD amongst locations).

Forest biome: Stratification by vegetation structure at fine scales

Snow disappearance date was later at higher elevations and in canopy gaps, while understory vegetation structure had little effect (Figure 3A). We also found that the effect of fine-scale differences in canopy structure (gaps vs. non-gaps) on snow disappearance date was similar to the effects of coarse-scale differences in elevation (100 m elevation differences) (Figure 4A). Thus, snow disappearance date differed as much at fine scales (where locations differed in forest canopy structure) as it did over coarse spatial scales.

As expected, growing season soil temperature generally declined with increasing elevation. Canopy gaps had higher maximum temperatures, but lower minimum and mean temperatures relative to non-gaps (Figure 3B–D). Canopy structure had a similar or greater effect on temperature than a 100 m change in elevation for average daily maximum and minimum temperature (Figure 4C, D). Locations where understory vegetation was removed experienced higher maximum and mean temperatures, but lower minimum temperatures, relative to control plots where vegetation was undisturbed (Figure 3B–D). Understory structure had a greater effect on average daily maximum temperature than a 100 m change in elevation, but had weaker effects on average daily mean and minimum temperature (Figure 4B–D). Overall, there was about as much heterogeneity in temperature at fine scales (differing vegetation structure) as there was at coarse scales (100 m differences in elevation).

Subalpine/alpine biomes: stratification by topographic position at fine scales

Snow disappearance date was later on the south side of the mountain, at higher elevations and in topographic depressions (Figure 3A). Furthermore, the effect of fine-scale topographic differences (depressions vs. ridges) on snow disappearance date was similar to the effects of coarse-scale differences in elevation (100 m difference in elevation) and side of the mountain

(Figure 4E). In other words, snow disappearance date differed as much over fine spatial scales as it did over coarse spatial scales.

Growing season soil temperatures during our sampling period were lower on the northeast side of the mountain than on the northwest and south sides, potentially because the meadows are at higher elevations on this side of the mountain. On a given side of the mountain, higher elevations (the upper limit of alpine meadows) had higher mean and maximum temperatures, but lower minimum temperatures, than lower elevations (the lower limit of the subalpine biome). Compared to ridges, depressions had higher mean and maximum temperatures but lower minimum temperatures (Figure 3B–D). We found that the effects of fine-scale topographic differences (depressions vs. ridges) were similar to the effects of coarse-scale differences in elevation and side of the mountain for average daily mean, maximum and minimum temperature (Figure 4F–H). Overall, there was as much heterogeneity in temperature at fine scales as there was at coarse scales.

Several microclimate variables were significantly correlated with vegetation characteristics (Figure 5). At study sites near the lower limit of the subalpine biome, percent cover by tree canopy was lower where snow disappearance date was later and average daily mean and maximum soil temperatures were higher ($p < 0.0001$). At study sites near the upper limit of alpine meadows, percent cover by ground vegetation was lower where snow disappearance date was later and average daily minimum soil temperature was lower ($p < 0.0001$).

Discussion

Our study suggests that climatic heterogeneity at the fine spatial scales most organisms experience their environment is substantial, implying that projections based on coarse-scale climate models will not capture the full complexity of range shifts in response to climate change. Specifically, we found large differences in snow disappearance date and growing season soil temperatures over small distances (Figures 3, 4), differences that were sometimes as large as those experienced when travelling hundreds of meters upward in elevation or several kilometers to a different side of the mountain. These microclimate variables have been shown to be strongly associated with plant species distributions and abundances (Wipf and Rixen 2010, Scherrer and Körner 2011), suggesting that the microclimate heterogeneity we observed is important for plant communities. We also found that vegetation characteristics (canopy and ground vegetation cover) can be strongly correlated with the microclimate variables influenced by fine-scale topographic features (Figure 5), further suggesting that the fine-scale climatic heterogeneity we observed is ecologically important. However, because we did not measure species distributions or abundances in this study, we cannot conclusively state that the microclimate heterogeneity we observed is linked to species distributions or abundances at Mount Rainier. Nonetheless, understanding fine-scale climatic heterogeneity will likely be critical for management, as cool or snowy microhabitats could provide an important buffer against the negative effects of climate change on biodiversity. Thus, when assessing potential species range shifts in response to climate change, it is critical for ecologists to consider fine-scale patterns in climate in addition to other important factors such as broad-scale climate patterns, dispersal constraints, biotic interactions and evolutionary dynamics.

Explanations of fine-scale climatic heterogeneity

In the forest biome, a complex interplay between elevation and vegetation structure is likely responsible for the heterogeneous patterns in snow disappearance date and soil temperature we observed. For example, locations under tree canopy gaps likely experienced later snow disappearance dates than locations under an intact canopy (Figure 3A) because tree canopies intercept snowfall where it can rapidly sublimate or melt instead of being incorporated into the snowpack on the ground (Varhola et al. 2010). Tree canopies also increase incoming longwave radiation (which increases ablation rates) and this effect can sometimes be greater than the effect of canopies decreasing incoming shortwave radiation by shading the snowpack (which reduces ablation rates), leading to a net effect of canopies increasing ablation rates (Sicart et al. 2004). Although the presence of trees has also been shown to lead to longer snow persistence by shading the snowpack and decreasing wind speeds (reducing incoming sensible and latent heat fluxes) (Varhola et al. 2010), these effects appear to be relatively weak at our study sites. Increased shading from tree canopies and understory vegetation in forest locations probably led to substantially lower maximum soil temperatures (Figure 3C). But these low sky exposure locations also experienced higher minimum soil temperatures (Figure 3D), probably due to vegetation emitting more longwave radiation (which warms the surface) than the night sky (Geiger et al. 2009). Differences in mean soil temperatures appeared to be the net effect of these two counteracting influences of sky exposure, with mean soil temperatures being higher in the shadier non-gap locations, but lower in the shadier undisturbed understory vegetation locations (Figure 3B).

Similarly, in the subalpine/alpine biomes we found that both coarse- and fine-scale features had large effects on climate. For example, snow disappeared substantially later from depressions in the landscape than from ridges only ~20 m away, likely because snow typically collects in these depressions while it is blown off of ridges and because shading from surrounding slopes can reduce ablation rates (Clark et al. 2011). Feedbacks between vegetation and climate are also likely to influence fine-scale climatic variability. At the lower elevation sites, for example, patches of trees with trunks sticking out above the snowpack emit substantial amounts of longwave radiation which quickens the ablation of snow next to the tree patch and can lead to earlier snow disappearance dates. Trees can also intercept snowfall, reducing snowpack accumulation under canopy and resulting in earlier snow disappearance (Varhola et al. 2010). These effects can lead to a positive feedback, where trees establish in microsites with earlier snow disappearance dates (e.g. ridges), and the established trees lead to even earlier snow disappearance dates and more tree establishment. This result is consistent with previous studies from subalpine meadows in the region that have documented increased tree establishment on ridges that tend to have earlier snow disappearance dates (Rochefort and Peterson 1996, Zald et al. 2012).

A striking pattern to emerge from our data was that mean and maximum soil temperatures were greater at higher elevations within the subalpine/alpine biomes (though minimum soil temperatures were lower). Feedbacks between climate and vegetation likely play important roles in producing this temperature pattern. First, tree cover declines with increasing elevation, leading to less shading and potentially higher daytime soil temperatures, especially during the sunny growing season when our data were collected. This explanation is supported by the negative correlation we observed between percent canopy cover (a measure of tree density) and mean/maximum soil temperature in the subalpine/alpine biomes (Figure 5B, C). Second, ground vegetation density declines with increasing elevation, which can lead to lower organic matter content in the soil and lower soil moisture levels. The lower moisture levels probably cause the soil to have a lower heat capacity, leading to greater temperature change per unit of energy input and hence higher maximum temperatures and lower minimum temperatures. This second explanation is supported by the pattern of low soil organic matter content and soil water holding capacity at high elevations in Mount Rainier's subalpine/alpine biomes (Appendix B). Soil characteristics also have important effects on vegetation in subalpine/alpine environments (Körner 2003), creating the possibility for complex feedbacks amongst soil, vegetation and climate. These two hypotheses are not mutually exclusive, and further study is needed to assess the importance of each. Regardless, our results suggest that even if patterns in climate are ultimately responsible for patterns in vegetation, the feedback effect of vegetation on soil temperature (either directly, or indirectly through the effects of vegetation on soil characteristics which then affect temperature) appears to at times be stronger than the original forcing of physiographic effects on soil temperature.

Implications of fine-scale climatic heterogeneity for species distributions in a warming world

Since snow disappearance date and growing season temperature vary dramatically over short distances, species whose distributions are primarily constrained by these climate variables may not need to migrate long distances to remain in suitable habitat even when there are large changes in climate. For example, in the subalpine/alpine biomes we found that the average difference in snow disappearance date between depressions and ridges separated by only ~20 m was often one month or more. This is an especially large difference considering the ground is typically only free of snow for 3-5 months out of the year at these elevations. Snow manipulation experiments have shown that differences of this magnitude have large impacts on the phenology, species composition, diversity and productivity of plant communities (Wipf and Rixen 2010).

Thus, these snowy microhabitats have the potential to serve as refugia for species in a warmer world and provide linkages to new areas of suitable climate, implying that fine-scale climatic heterogeneity could buffer species from climate change (Scherrer and Körner 2010, Dobrowski 2011, Keppel et al. 2012), as it may have done during past periods of rapid climate change (Hof et al. 2011). Given that we did not stratify our sensors along all gradients likely to produce fine-scale differences in climate (e.g. wind direction, aspect – Geiger et al. 2009, Clark et al. 2011), our results may even be an underestimate of the magnitude of fine-scale heterogeneity.

The importance of topographic heterogeneity for creating climatic heterogeneity shown in this study and others (Ackerly et al. 2010, Scherrer and Körner 2011, Fridley 2009, Millar and Westfall 2010, Scherrer and Körner 2010, Wundram et al. 2010) also suggests that mountainous regions will be important for providing climatic refugia in a warming world. However, mountain biotas will still likely face unique challenges. For example, organisms currently living on or near summits will not be able to shift upwards to track suitable climate, and deep valleys between mountains will likely pose serious obstacles to poleward shifts (Fischlin et al. 2007). Broad-scale modeling will continue to be important for addressing these problems. Furthermore, fine-scale environmental heterogeneity does not guarantee that biodiversity will be buffered from climate change. It is possible for heterogeneity to produce small, isolated patches of habitat that cannot support many species, producing a negative effect on diversity (Tamme et al. 2010). Thus, whether the net effect of heterogeneity on maintaining diversity will be positive during a period of rapid climate change remains an open question.

Different kinds of cool or snowy microhabitats will likely differ in their effectiveness as refugia in a warming world. First, the abundance of microhabitat types will strongly influence how effective they can be as refugia. For example, depressions in the landscape in the subalpine/alpine biomes may have a high likelihood of serving as refugia because they are a common topographic feature. Second, the longevity of microhabitat types will affect their ability to act as refugia. For example, canopy gaps may disappear relatively quickly as trees establish in them, forcing species that might use gaps as refugia to migrate amongst gaps, which may not be possible for some species (though others may be adapted to this migration). In contrast, depressions in the landscape could provide more long-term refugia. Third, the temporal climatic heterogeneity experienced in microhabitat types may affect how well they can serve as refugia. For example, gaps had lower daily minimum and higher daily maximum temperatures compared to non-gaps, showing that these microhabitats experience a wide variety of temperatures. This heterogeneity may favor some species but not others. A final complicating factor influencing how and whether microhabitat types can serve as climatic refugia are the non-climatic conditions associated with them. For example, depressions may differ from other topographic positions in soil characteristics, which could prevent some species from using them as snowy microrefugia.

An important caveat to these findings is that they are based on one year of data. Spatial patterns in climate can change from year to year due to differences in prevailing synoptic weather patterns (Lundquist and Cayan 2007, Bennie et al. 2010, Lundquist et al. 2010), so the patterns we observed in the year we conducted this study may not represent typical spatial patterns. However, the year of our study was a fairly typical year in terms of snow disappearance date and in terms of growing season air temperature for the past few decades (Appendix C). And although spatial patterns in climate can vary year to year, the patterns are generally constant from one year to the next, especially in terms of snow (Erickson et al. 2005, Deems et al. 2008, Sturm and Wagner 2010, Egli et al. 2012). For example, locations with later snow disappearance dates in one year tend to have later snow disappearance dates in other years, even though the spatially averaged snow disappearance date varies from year to year.

Challenges and opportunities for management

To best protect biodiversity in a period of rapid climate change, conservation biologists and resource managers will require realistic assessments of future species distributions (Hannah et al. 2007). Thus, incorporating fine-scale climatic heterogeneity is essential for improving projections of species range shifts and extinction risks. Current coarse-scale models of the relationships between climate and species distributions ignore fine-scale heterogeneity and may therefore overestimate the distance species must migrate to track suitable climate (because forecasted range shifts are necessarily at the resolution of the model), and overpredict habitat loss and extinction risks (Austin and Van Niel 2011, Barrows and Murphy-Mariscal 2012, Luoto and Heikkinen 2008, Randin et al. 2009, but see Trivedi et al. 2008). Ecologists have previously criticized these bioclimate envelope models for only predicting where the climate that is currently associated with a species distribution will shift to and failing to account for biotic factors that could affect a species' ability to track these climate shifts (dispersal limitations, biotic interactions and evolutionary changes) (Pearson and Dawson 2003). However, the limitation of model spatial resolution could undermine predictions not only of species' abilities to track shifts in climate but also of the climate shifts themselves.

In addition to more realistically forecasting range shifts, knowledge of fine-scale climatic heterogeneity may also allow managers to increase species and ecosystem resilience to climate change. For example, protecting microhabitats with cooler temperatures or later snow disappearance dates could become increasingly important as climate change occurs because these microhabitats may provide critical refugia for species. Additionally, our results suggest that planting seedlings and sowing seeds at a variety of microhabitats when restoring degraded sites is an important bet-hedging strategy because it could increase the probability that species establish in microsites that remain suitable as climate change progresses, even if those microsites are only marginally suitable now. Thus, information on fine-scale climate heterogeneity has the potential to be useful for natural area protection and restoration when taken together with other important factors such as edaphic constraints, biotic interactions, genetic diversity and financial costs (Rochefort et al. 2006). More detailed and longer term studies are needed to assess whether microclimate heterogeneity can contribute substantially to plant establishment and restoration efforts in a warming world.

Conclusions

We have shown that snow disappearance date and growing season soil temperature vary dramatically over small distances due to differences in vegetation structure and topography. In fact, fine-scale features such as gaps in the forest canopy or small depressions in the landscape can produce differences in snow disappearance date and soil temperature as large as those produced by shifting hundreds of meters up a mountain slope. This large degree of fine-scale spatial heterogeneity may provide an important buffer against the negative effects of rapid climate change, as many species may only need to migrate tens of meters from one microhabitat to another in order to track suitable climate, as opposed to shifting hundreds of meters upward in elevation or hundreds of kilometers poleward. Climate change will undoubtedly pose serious threats to biodiversity, but knowledge of fine-scale climatic heterogeneity may allow managers to better assess and potentially alleviate some of these threats.

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Tables

Table 1. Details of temperature sensor deployment.

Biome(s)	**Time span of deployment**	**# sites**	**# sensors per site**	**Total # sensors**	**Type of sensor**	**Sensor accuracy**	**Data logging interval**	**Sensor location**
Forest	Summer 2009-Fall 2010	3	8	24	HOBO Pendants made by the Onset Computer Corporation	±0.53°C from 0° to 50°C	2 hours	Soil surface
Forest	Summer-Fall 2010	7[*]	20	140	HOBO Pendants made by the Onset Computer Corporation	±0.53°C from 0° to 50°C	1 hour	Soil surface
Subalpine/ alpine	Summer 2009-Summer 2010	6	24	144	iButtons made by Maxim Integrated Products	±0.5°C from -10° to 65°C, or ±1°C from -30° to 70°C[†]	1, 2 or 4 hours[†]	3 cm below soil surface

[*] These sites include the three sites with sensors deployed in Summer 2009.
[†] Differences in accuracy and logging intervals were due to differences in the specific model of iButton sensor used.

Table 2. Best-fit models for the climatic response variables.

Study	**Climatic response variable**	**Model formula***	**r^2**
Forest: stratification by vegetation structure	Snow disappearance date	SDD = *f* { **elev** + **canopy** + understory[†]+ (1|pair) }	0.94
Forest: stratification by vegetation structure	Average daily mean temperature	Tmean = *f* { **elev** + canopy + understory + elev:canopy + **elev:understory** + **canopy:understory** + (0+canopy|pair) }	0.35
Forest: stratification by vegetation structure	Average daily maximum temperature	Tmax = *f* { elev + **canopy** + understory + **elev:canopy** + **elev:understory** + **canopy:understory** + (0+canopy|pair) }	0.40
Forest: stratification by vegetation structure	Average daily minimum temperature	Tmin = *f* { **elev** + canopy + **understory** + **elev:canopy** + **canopy:understory** + (0+canopy|pair) }	0.20
Subalpine/alpine: stratification by topographic position	Snow disappearance date	SDD = *f* { **side** + **elev** + **topo** + **elev:topo** + **side:elev** + (1|tran) }	0.60
Subalpine/alpine: stratification by topographic position	Average daily mean temperature	Tmean = *f* { **side** + elev + topo + **elev:topo** + **side:elev** }	0.60
Subalpine/alpine: stratification by topographic position	Average daily maximum temperature	Tmax = *f* { **side** + elev + topo + **elev:topo** + **side:elev** }	0.52
Subalpine/alpine: stratification by topographic position	Average daily minimum temperature	Tmin = *f* { side + elev + **topo** + side:elev }	0.30

*****Parameters in bold have significant coefficients ($p < 0.05$). For the forest biome study, elev = elevation; canopy = forest canopy structure, gap or non-gap; understory = understory vegetation structure, removed or control; pair = gap/non-gap pairings. For the subalpine/alpine biomes study, side = side of the mountain, south or northwest or northeast; elev = elevation; topo = topographic position, ridge or depression; tran = sensor deployment transect. The colon indicates an interaction effect between two explanatory variables. The parentheses indicate the term is a random effect – all other terms are fixed effects. If *fe* is a particular fixed effect and *re* is a particular random effect, then (1|*re*) indicates the intercept was allowed to vary randomly with respect to *re* while (0+*fe*|*re*) indicates the interaction of *fe* and *re* was allowed to vary randomly. The case of both the intercept and interaction being allowed to vary randomly was not included in any of the best-fit models.

[†] Understory was not included in the best-fit model, based on AIC, but was retained for comparative purposes.

Figures

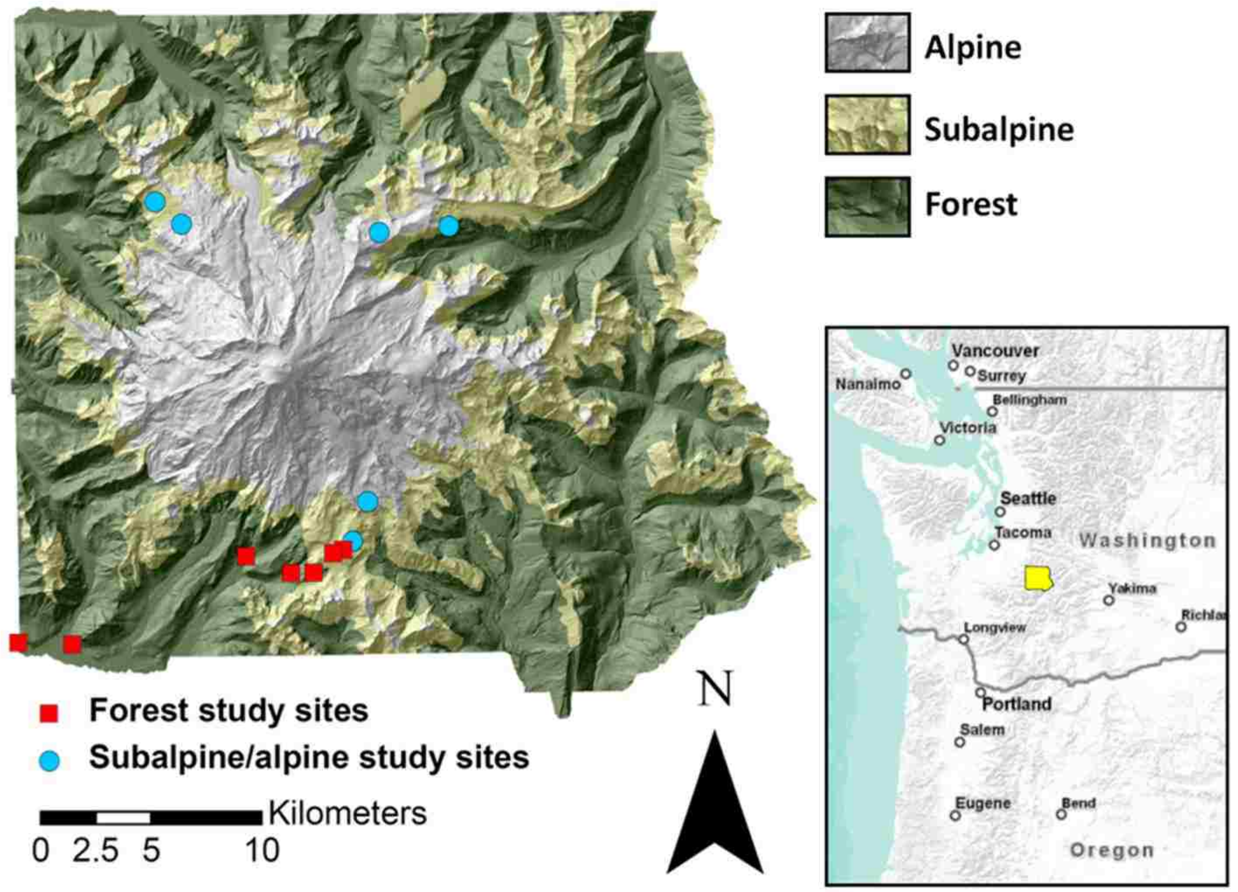

Figure 1. Study area. Mount Rainier National Park and its three major biomes, along with study site locations. Shading depicts topographic relief.

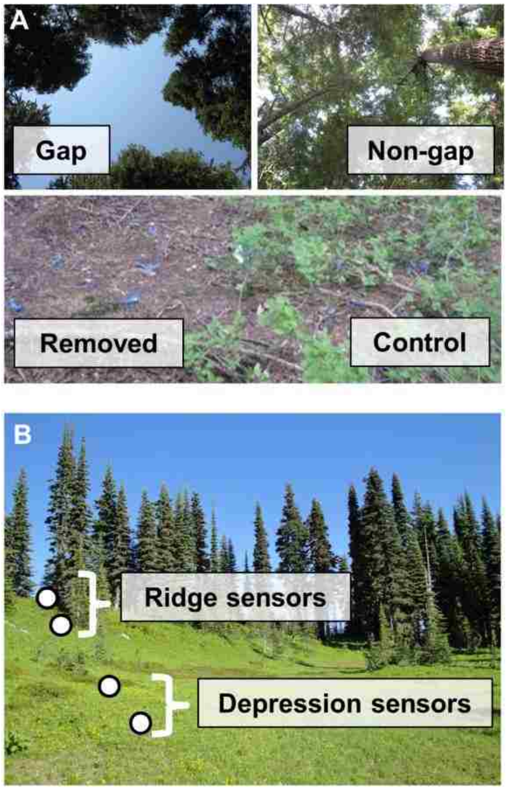

Figure 2. Temperature sensor deployment. Sensor deployment in (A) forest and (B) subalpine/alpine biomes. At each elevation in the forest biome (A), sensors were placed in gaps in the forest canopy (top left) and non-gaps with intact forest canopy (top right). Within each of these canopy types, sensors were located in plots where understory vegetation was removed (bottom left) and control plots where it was left undisturbed (bottom right). In the subalpine/alpine biomes (B), temperature sensors were located along transects running from depressions in the landscape to ridges.

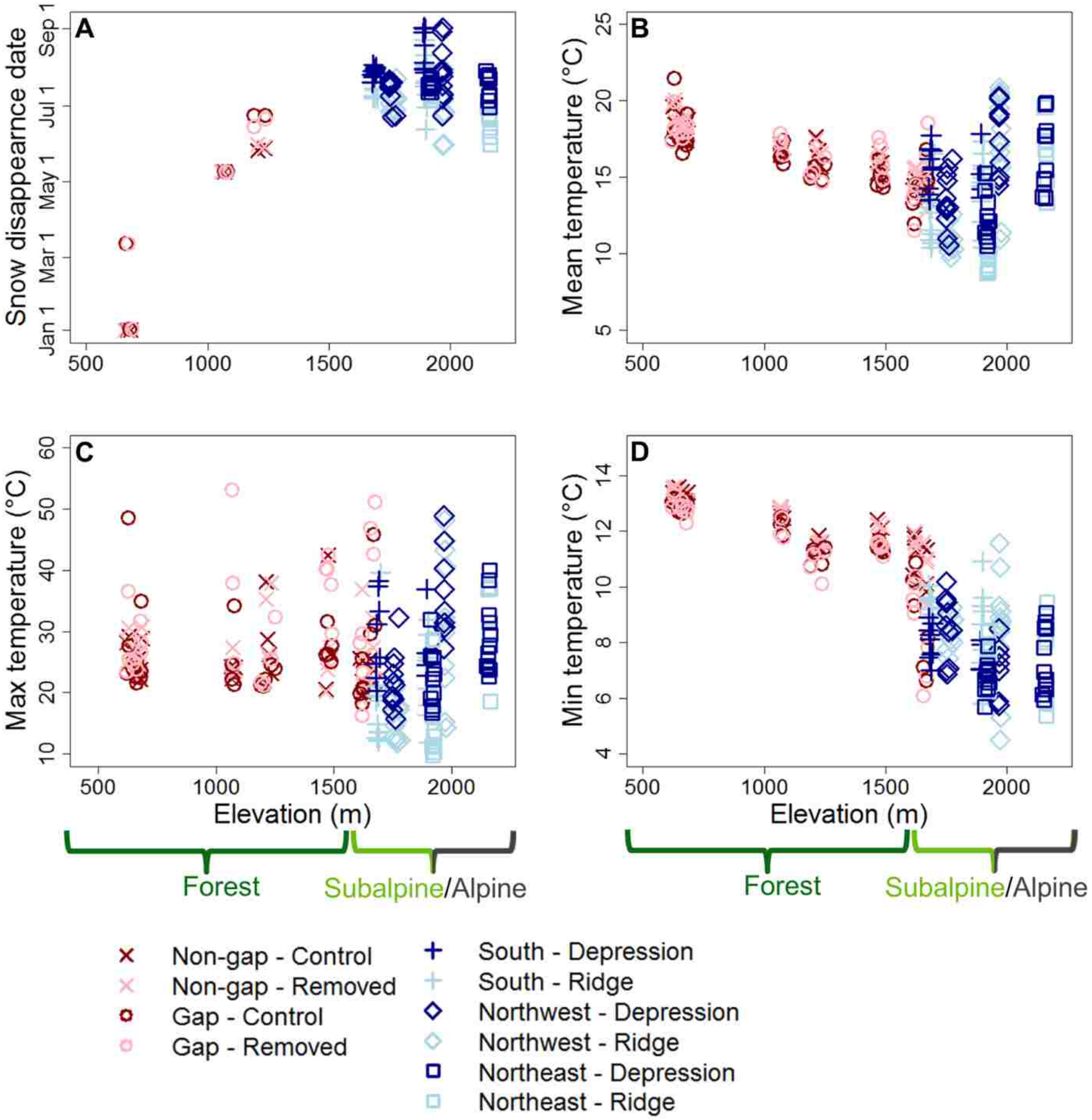

Figure 3. Patterns in climate. (A) Snow disappearance date in 2010 and average daily (B) mean, (C) maximum and (D) minimum soil temperature for a representative week during the growing season (August 11-18, 2010) plotted against elevation. Note the differences in scale on the axes showing temperature values. Points represent individual sensors with symbol type and color designating sampling stratification for forest (dark and light red) and subalpine/alpine sites (dark and light blue). “Non-gap”/“gap” refer to canopy structure categories while “control”/“removed” refer to understory structure categories (forest sites). “South”/“northwest”/“northeast” refer to sides of the mountain while “ridge”/“depression” refer to topographic positions (subalpine/alpine sites). Approximate biome ranges are shown below the elevation axes.

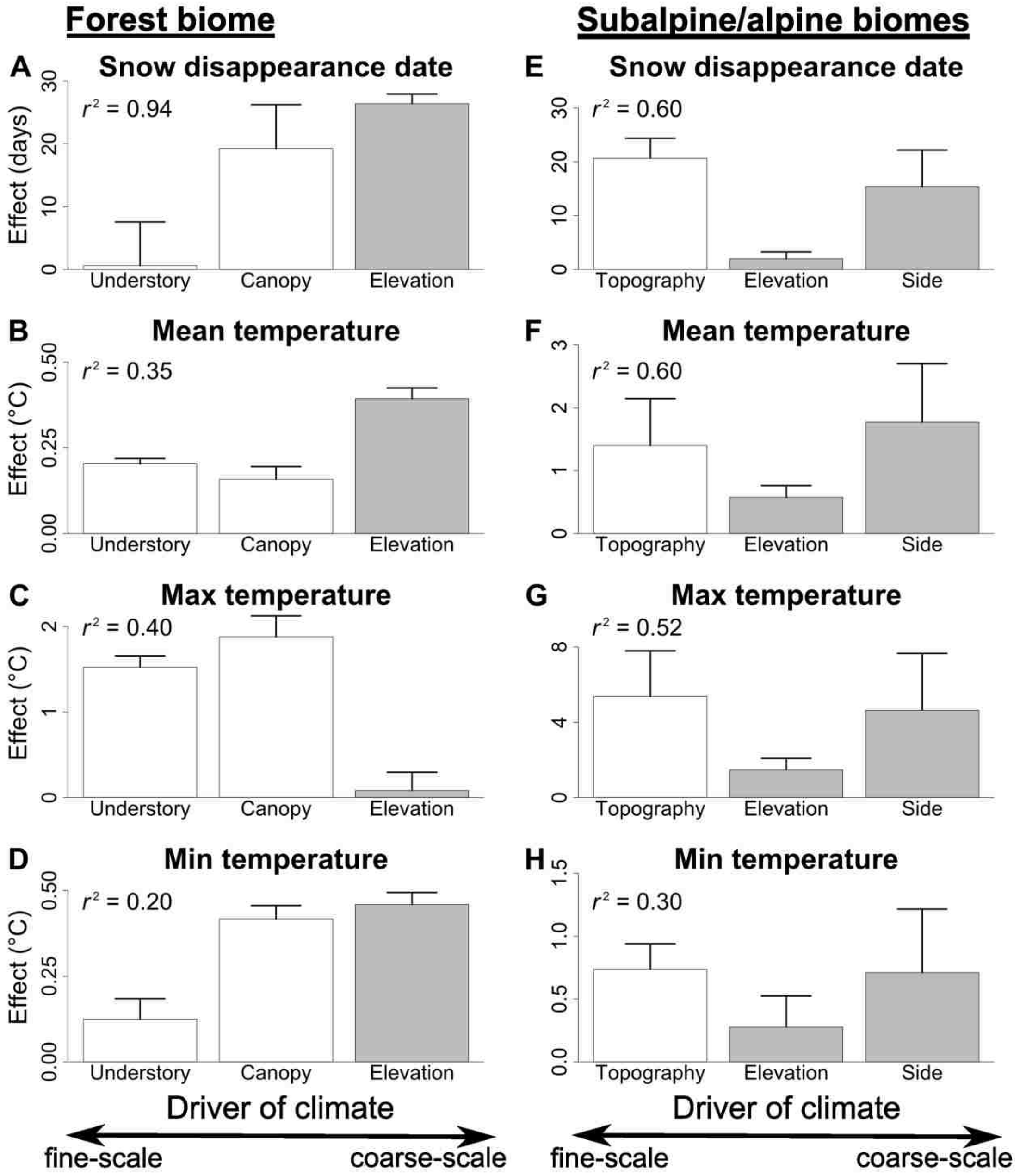

Figure 4. Effects of fine- and coarse-scale drivers of climate. The effects of fine- and coarse-scale drivers of climate on snow disappearance date and the average daily values of mean, maximum and minimum growing season soil temperature. Bars show differences in snow disappearance date or temperature attributed to the effect of different drivers of climate by the best-fit model, with standard error. The effect of elevation was standardized to the effect of a 100 m difference in elevation. Bars filled with gray represent drivers that are coarse enough in scale to be captured by typical climate models (>1 km) while unfilled bars represent drivers too fine in scale to be captured by these models (≤20 m). Fine-scale drivers of climate often had a greater effect on snow or soil temperature than coarse-scale drivers.

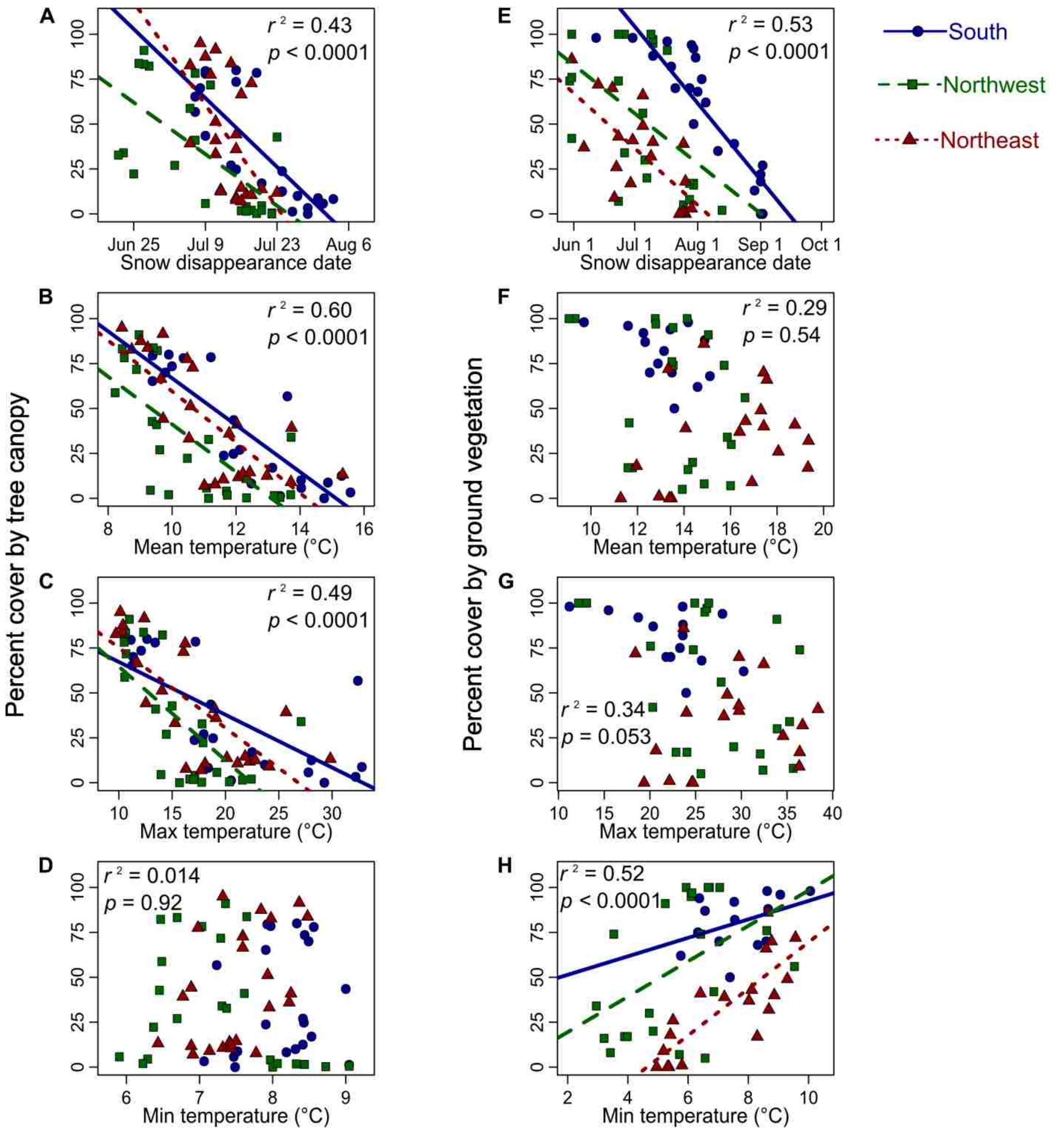

Figure 5. Relationships between vegetation characteristics and microclimate. (A-D) Percent cover by tree canopy at sites near the lower limit of the subalpine biome and (E-H) percent cover by ground vegetation at sites near the upper limit of alpine meadows plotted against the four microclimate variables (snow disappearance date and average daily mean, maximum and minimum soil temperature) on each of the three sides of the mountain. The r^2 values are for models that included the microclimate variable and side of the mountain as explanatory variables, while the *p* values indicate the significance of the microclimate variable in these models. Regression lines are shown for significant *p* values (< 0.05).

Supporting information

Appendix A. Model fitting and selection procedure

We used linear mixed effects models (LMMs) with gap/non-gap pair (for the forest biome) or transect (for the subalpine/alpine biomes) designated as a random effect to characterize the relationships between the explanatory variables and the four climatic response variables (snow disappearance date and average daily mean, maximum and minimum growing season soil temperature). For each climatic variable in either the forest or subalpine/alpine biomes, we used a three-step process to select the "best-fit" combination of random and fixed effects for the model following (Zuur et al. 2009).

First, we determined the optimal random effects structure by using restricted maximum likelihood estimation to fit several LMMs which included main effect terms for all explanatory variables and terms for all two-way interactions, as well as different combinations of random effect terms (random intercepts only, random slopes only, or both random intercepts and random slopes). Then we calculated the Akaike's information criterion (AIC) value for each LMM to identify the best-fitting model by choosing the model with the lowest AIC or the model with the fewest parameters when AIC values of the lowest AIC model and other candidate models differed by less than 2 AIC units (Burnham and Anderson 2002). If the estimated variance explained by the random effects was zero, we used a model with only fixed effects, i.e. a linear model (LM).

Second, we determined the optimal fixed effects structure by creating models with all possible combinations of fixed effect terms (fit using maximum likelihood estimation) but sharing the same optimal random effects structure selected in the first step (which could be no random effects). We then calculated the AIC value for each model and selected the model with the lowest AIC or the model with the fewest parameters when AIC values of the lowest AIC model and other candidate models differed by less than 2 AIC units (Burnham and Anderson 2002).

Third, we fit a model using restricted maximum likelihood estimation for LMMs and maximum likelihood estimation for LMs with the random effects structure selected in the first step (which could be no random effects) and the fixed effects structure selected in the second step. We considered this model to be our final “best-fit” model. All models were fit in R version 2.12.0 (R Development Core Team 2010) and the LMMs were fit using the lme4 package (Bates et al. 2011).

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Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer, New York.

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Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.

Appendix B. Soil characteristics in the subalpine and alpine biomes

To characterize spatial patterns in soil organic matter content and water holding capacity in the subalpine and alpine biomes, we collected soil samples from seven plots along an elevation transect from the upper limit of the forest biome up to the lower limit of the alpine biome on the south side of Mount Rainer. Within each plot, we sampled from six locations differing in topographic position – two ridges, two depressions and two slopes – for a total of 42 samples for both organic matter content and water holding capacity tests.

To calculate soil organic matter content (the proportion of organic material in the soil), we first dried the sample to remove all moisture, recorded the mass of the dry soil, placed the dried soil in a muffle furnace set to 400°C for 10 hours to volatilize all organic matter and then recorded the mass of the remaining unburned soil. We subtracted the mass of the unburned soil from the mass of the dried soil to obtain the mass of the organic matter in the sample. We then calculated organic matter content as the mass of organic matter in the sample divided by the mass of the dried soil sample.

To calculate soil water holding capacity, we dried each sample to remove all moisture, recorded the mass of the dry soil, saturated the soil with water and then recorded the mass of the wet soil. We subtracted the mass of the dry soil from the mass of the wet soil to obtain the mass of the water held by the soil. We then calculated soil water holding capacity as the mass of the water held by the soil divided by the mass of the dry soil.

We used generalized linear models to test the importance of elevation, topographic position and their interaction on organic matter content (Beta error distribution) and soil water holding capacity (Gamma error distribution). The best-fit model for both soil variables included elevation but not topographic position or the interaction of elevation and topographic position (based on AIC – Akaike's information criterion). To assess the significance of pairwise differences in organic matter content and soil water holding capacity amongst elevations, we performed multiple comparison tests in R version 2.12.0 (R Development Core Team 2010) using the multcomp package (Hothorn et al. 2008). Both organic matter content and soil water holding capacity are lower at higher elevations and seem to cross a threshold around 1900 m, the upper ecotone of the subalpine biome (Figure B1). Below 1900 m the ground is mostly covered in vegetation, while above 1900 m it is mostly bare.

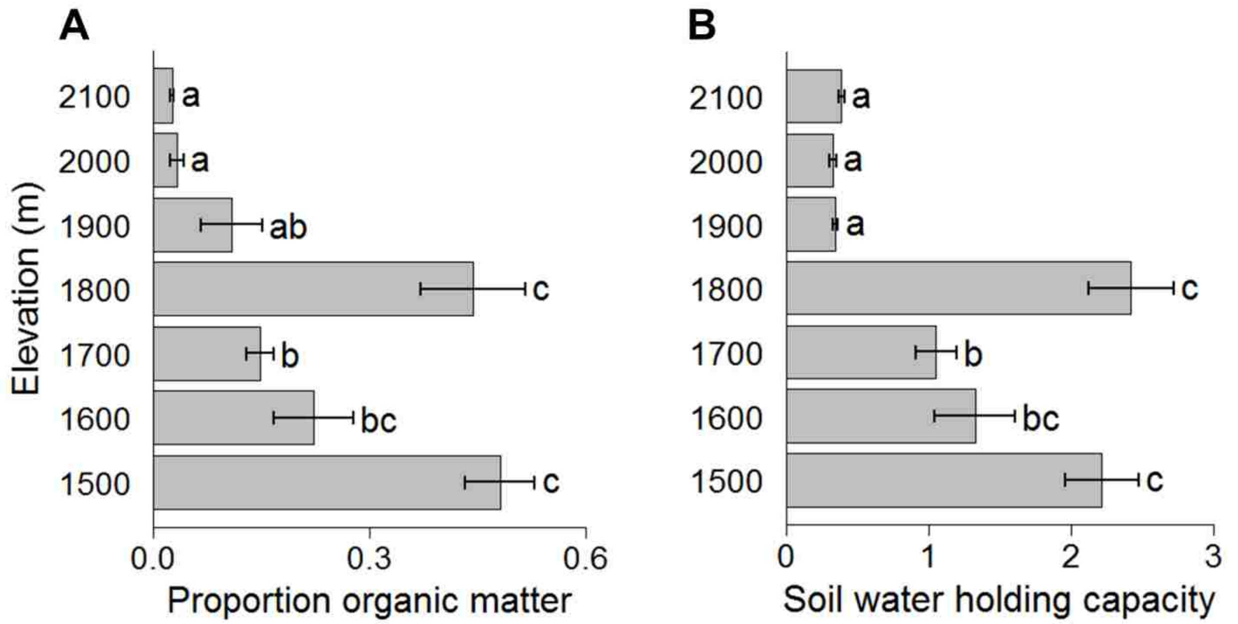

Figure B1. Mean soil characteristics across elevation. Bars with same letter are not significantly different (multiple comparison test, $\alpha = 0.05$). Error bars show standard error.

Literature cited

Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. Biometrical Journal 50:346-363.

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Appendix C. Climatological context of the study

Data from a climate station located in Mount Rainier National Park at 1564 m elevation (the Paradise SNOTEL site, www.wcc.nrcs.usda.gov/snow) indicate that 2010, the year microclimate data were collected for this study, was a fairly typical year in terms of snow disappearance date and growing season air temperature for the past few decades. Snow disappearance date at this station for 2010 was within one standard deviation of the average snow disappearance date for 1984-2010 (Figure C1). Average daily mean, maximum and minimum air temperatures for the periods we analyzed soil temperatures in 2010 were all within one standard deviation of the 1984-2010 averages, with the single exception of average daily maximum temperature for the forest biome sampling period, which was 1.8°C lower than average. If typical values of climate variables at the climate station are associated with typical spatial patterns of climate variables in the Park, the patterns we observed in 2010 are likely representative of what typically occurs.

To further assess whether spatial patterns in snow disappearance date might vary year to year in the Pacific Northwest, we assessed spatial patterns in snow disappearance dates at snow monitoring stations in the region (SNOTEL sites). We found that spatial patterns in snow disappearance data in 2010 were not qualitatively different from typical years (the 1982-2011 climatology), or from low or high snow years (Figure C2). These spatial patterns are on a much coarser scale than our study, but are consistent with the findings of other fine-scale studies that spatial patterns in snow disappearance dates do not differ greatly year to year (Erickson et al. 2005, Deems et al. 2008, Sturm and Wagner 2010, Egli et al. 2012).

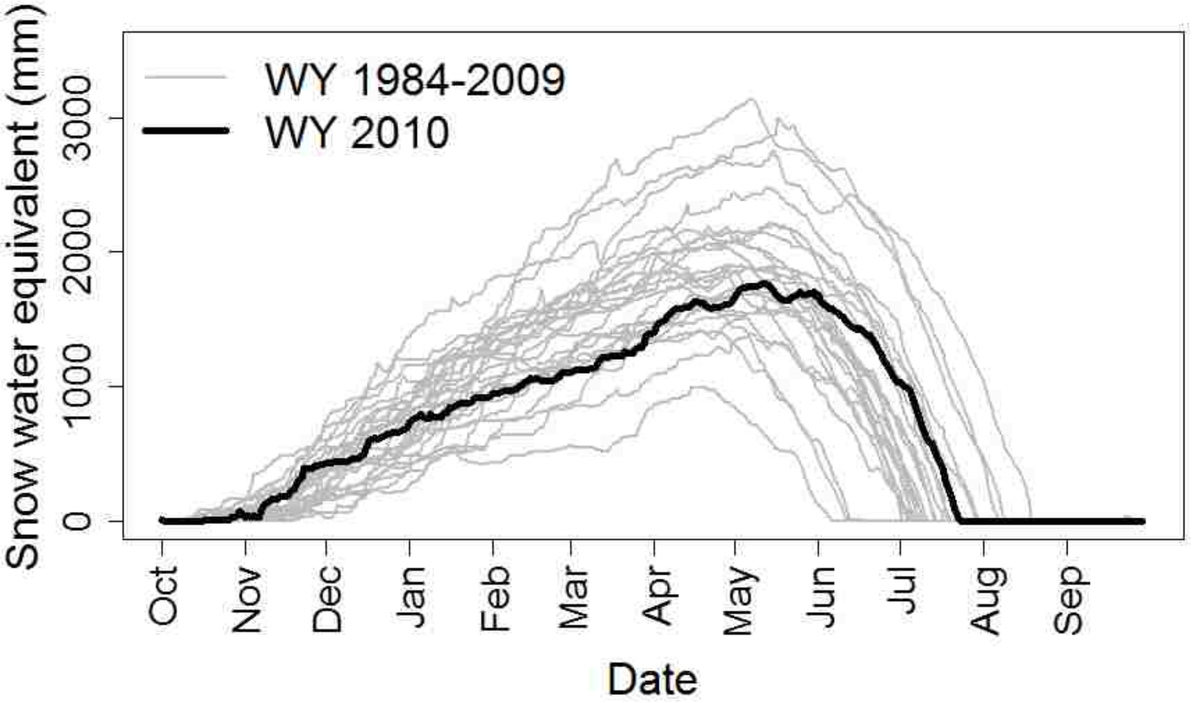

Figure C1. Year-to-year variation in snow at Mount Rainier. Data are from the Paradise SNOTEL site. Snow water equivalent is the amount of water contained in the snowpack, and represents the depth of water that would result if the snow melted. The years are water years, which run from October 1 of the previous year to September 30 of the given year (e.g. water year 2010 ran from October 1, 2009 to September 30, 2010).

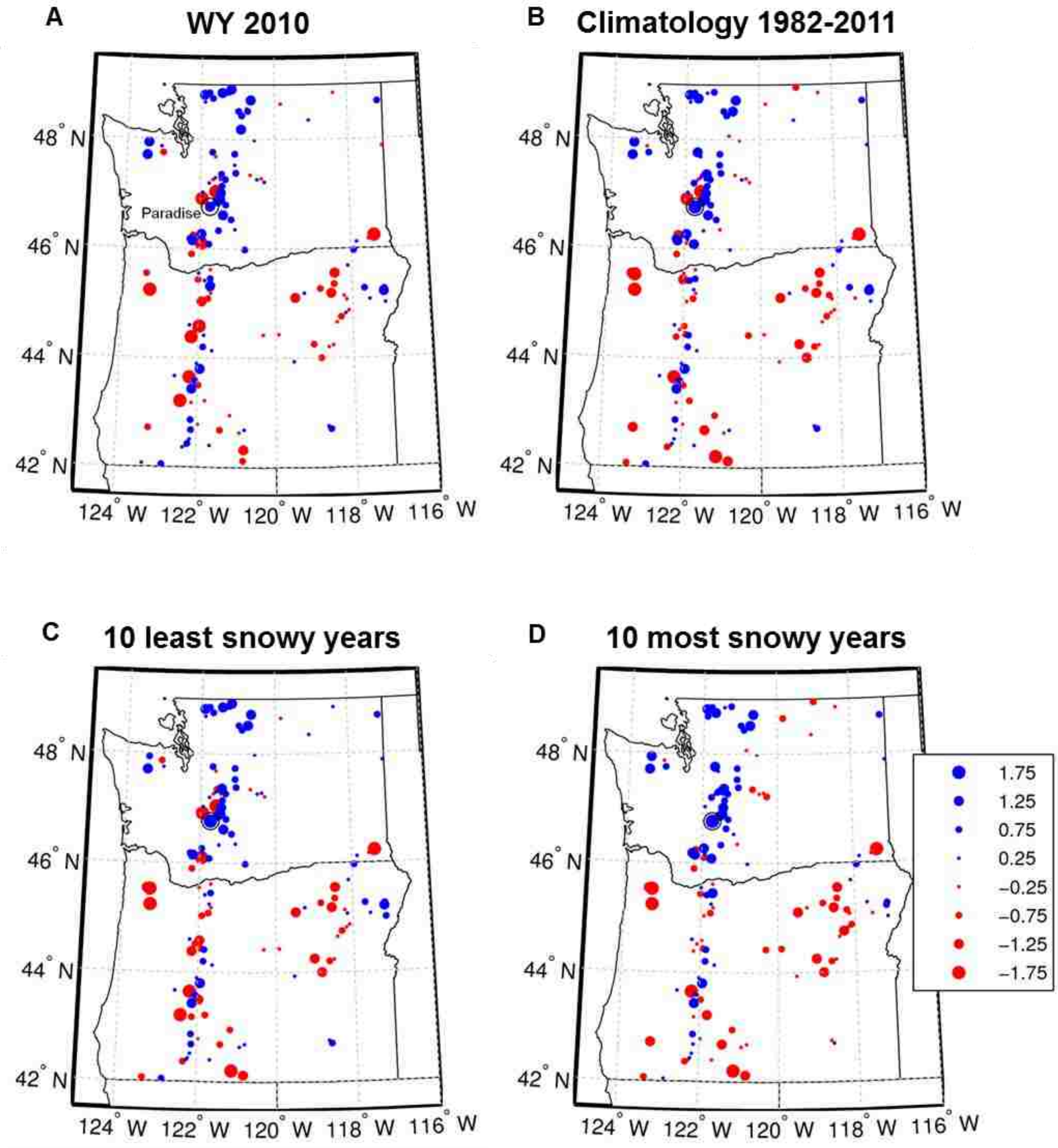

Figure C2. Spatial patterns in snow disappearance dates over time in Washington and Oregon. The dots represent snow monitoring stations (SNOTEL sites), with the station nearest to the study sites circled (Paradise). The size and color of the dots indicate how many standard deviations each station's snow disappearance date is from the mean snow disappearance date across all sites for the given time period, with blue representing later than average snow disappearance and red representing earlier. (A) Spatial patterns of snow disappearance date in 2010, (B) the average snow disappearance date patterns for 1982-2011, (C) the average snow disappearance date patterns for the 10 most snowy and (D) 10 least snowy years in the 1982-2011 period, with most and least snowy being based on the ranked peak snow accumulation value.

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Deems, J. S., S. R. Fassnacht, and K. J. Elder. 2008. Interannual consistency in fractal snow depth patterns at two Colorado mountain sites. Journal of Hydrometeorology 9:977-988.

Egli, L., T. Jonas, T. Gruenewald, M. Schirmer, and P. Burlando. 2012. Dynamics of snow ablation in a small Alpine catchment observed by repeated terrestrial laser scans. Hydrological Processes 26:1574-1585.

Erickson, T., M. Williams, and A. Winstral. 2005. Persistence of topographic controls on the spatial distribution of snow in rugged mountain terrain, Colorado, United States. Water Resources Research 41:W04014.

Sturm, M., and A. M. Wagner. 2010. Using repeated patterns in snow distribution modeling: An Arctic example. Water Resources Research 46:W12549.

Chapter 3: The interacting roles of climate and soil in plant species range shifts

Kevin R. Ford, Janneke Hille Ris Lambers

Abstract

Ecologists expect climate change to lead to species range shifts and predict these shifts will follow current climatic gradients such as those found across latitude and elevation. However, climate is not the only constraint on species distributions, and the influence of other environmental variables may lead to complex range shift dynamics that differ significantly from responses predicted on the basis of climate alone. We addressed these issues in the context of mountain biomes and examined the interaction of two important environmental drivers in this system: climate and soil. To do this, we conducted a seedling transplant experiment in which we exposed seedlings of tree, subalpine meadow and alpine meadow species to different combinations of climate and soil conditions to determine their joint influences on establishment success. Overall, we found that climate and soil had important and interacting effects on seedling establishment that may strongly influence range shift dynamics at the upper and lower limits of the subalpine/alpine meadows. Initial survival declined where snow disappeared earlier, likely due to greater water stress, with more severe and significant declines for seedlings in bare soils that have lower water holding capacity. These patterns imply that as climate change leads to earlier snow disappearance, initial seedling survival will decline, especially in bare soil. However, seedling size was typically greater where snow disappeared earlier, but only in meadow soils, suggesting the longer growing seasons brought by earlier snow disappearance will likely increase seedling growth, but primarily in meadows where soil resources are not limiting. Thus, as climate change progresses, seedlings in meadow soils are likely to achieve greater

establishment success compared to those in bare soils, because they will experience less of the negative effects of earlier snow disappearance on survival and more of the positive effects on growth. These establishment patterns suggest that lower elevation tree species establishing in meadows will undergo relatively rapid upward range expansions, at the expense of the shade-intolerant meadow species, while meadow plant species colonizing bare ground will experience relatively slow range expansions at their upper range limits. Together, the results indicate that meadow species will contract at their lower limits faster than they expand at their upper limits, possibly leading to reductions in the geographic extent of these species.

Introduction

Understanding the interaction of climatic and non-climatic constraints on species ranges is critical for predicting the dynamics of climate-change-induced range shifts. Climate plays a fundamental role in determining species geographic ranges (Sexton et al. 2009), and ongoing climate change has been associated with upward and poleward range shifts in taxa around the world (Chen et al. 2011). Rapid warming projected for the rest of the 21st century may result in even greater range shifts, potentially causing widespread loss of biodiversity and ecosystem services (Fischlin et al. 2007). However, climate is not the only determinant of species ranges, with biotic interactions, disturbance, soil and other factors also playing key roles (Gaston 2003, Gilman et al. 2010, HilleRisLambers et al. 2013). The interaction of these multiple drivers of species ranges can produce complex range shift dynamics in response to climate change that significantly differ from responses predicted on the basis of climate alone (Ibáñez et al. 2006).

The interplay of different range determinants may be especially important in mountain biomes, where the interaction of climate and soil constraints on seedling establishment has the potential to dramatically alter plant species range shifts. As one ascends mountain slopes, closed-canopy forests give way to subalpine and then alpine meadows, which give way to bare ground and ice. Along these same gradients, climate varies dramatically, with temperatures decreasing and snow duration increasing with elevation. With climate change, trees will likely establish in meadows (Harsch et al. 2009) while meadow plants establish on bare ground (Cannone et al. 2008, Gottfried et al. 2012, Pauli et al. 2012), leading to upward movement of species and biomes (forest, meadows). However, soil properties also vary drastically across elevation, with bare soils above the meadows having much lower organic matter content, water holding capacity and concentrations of key nutrients (particularly nitrogen) compared to lower elevation meadow soils (Körner 2003). And while climate is likely to change rapidly in the coming decades with rising temperatures and declining snow duration (Collins et al. 2013), soil development will likely be relatively slow and lag behind climate change (Körner 2003). Thus, seedling establishment above a species' current range may be inhibited by soil conditions even if the climate becomes suitable, so that range shifts fail to track shifts in climate.

To address the question of how climate, soil and their interaction influence seedling establishment in mountain biomes, we conducted a manipulative field experiment in which we exposed seedlings of tree, subalpine meadow and alpine species to different combinations of climate and soil conditions, and monitored seedling survival and size. Survival and size are both important for seedling establishment, with initial survival making establishment possible and greater growth and size leading to greater long-term survival and establishment (Harper 1977, Niinemets 2010). Specifically, we planted seedlings in plots spanning the elevational range of the meadows where we measured microclimate, and within each plot planted half the seedlings in soil collected from the meadows' lower margin ("meadow soil") and half in soil from bare ground above the meadows ("bare soil").

We hypothesized that survival and size would increase with earlier snow disappearance (which leads to longer growing seasons) and increasing temperature because plant performance is generally considered to be strongly energy-limited in these systems (Stephenson 1990, Körner and Paulsen 2004, Albright and Peterson 2013). We also expected survival and size to be greater for seedlings in meadow soil compared to bare soil due to the higher quality of meadow soil (which has higher water-holding capacity and concentrations of key nutrients). Furthermore, we hypothesized that seedlings in meadow soil would experience greater gains in survival and size with earlier snow disappearance and increasing temperature compared to seedlings in bare soil because seedlings in meadow soil would be less limited by soil factors and more able to benefit from the longer and warmer growing seasons. Such patterns in seedling establishment would imply that climate change could lead to trees expanding upward into meadows faster than meadow plants can expand onto bare ground. This dynamic could lead to a reduction in the ranges of meadow species that would face competition from rapidly invading lower elevation trees while experiencing only minor upward range expansions of their own (Figure 1).

Methods

Study system

Mount Rainier National Park encompasses 95,354 ha of land in the western Cascade Mountains in Washington State, USA. Elevation ranges from 518 m in the valley floors to 4392 m at the peak of Mount Rainier, the volcano located in the middle of the Park. The region experiences a temperate, maritime climate with mild, dry summers and cool, wet winters that produce large snowpacks. The mountainous terrain creates steep climatic gradients: temperature decreases and precipition increases with elevation. We conducted this study on the south side of Mount Rainier where forests predominate from lower elevations up to about 1500m, while subalpine and alpine meadows extend from 1500m to around 1900m, with patches of trees interspersed with the subalpine meadows. Above the meadows, the ground is mostly bare or glaciated, with a low density of alpine plants, mosses, lichens, algae and cryptobiotic soil crusts. We established six study sites along an elevational transect from 1490 – 2050 m, with one site roughly every 100 m in elevation. A climate station at 1654 m elevation near the transect reports a mean annual temperature of 3.7ºC and mean annual precipitation of 3005 mm (1981-2010 normals, NOAA National Climate Data Center).

Snow is an important driver of plant performance and distribution in this system because the duration of the annual snowpack stongly limits the length of the growing season (Franklin and Dyrness 1988). At a snow monitoring station near our study transect, snow disappears on July 17 and covers the ground about nine months (268 days) on average (for 1984-2013, NRCS SNOTEL data). Snow disappearance and duration is also highly variable spatially across elevation and topographic position (Ford et al. 2013), and year to year. In our study plots, snow disappearance date varied from June 6 to September 22, while snow duration varied from 8.5 months (205 days) to 11 months (333 days).

Focal species

We planted seedlings from seven different species that are all abundant in the subalpine or alpine meadows of Mount Rainier and represent important functional groups (Table 1). *Abies lasiocarpa* is the dominant tree species of the subalpine zone and responsible for the vast majority of observed tree encroachment in the Park's subalpine meadows (Rochefort and Peterson 1996). *Anemone occidentalis* (forb), *Lupinus arcticus* (nitrogen-fixing forb) and *Carex spectabilis* (graminoid) are abundant in the subalpine meadows. *Saxifraga tolmiei* (forb), *Lupinus lepidus* (nitrogen-fixing forb) and *Carex nigricans* (graminoid) are abundant in the higher elevation alpine zone.

Experimental design

In each fall from 2009-2011, we collected seeds of the focal species from along the elevational transect where the study sites were located, depending on availability (seed production varied enormously year-to-year for the focal species). We also collected soil from subalpine meadows at the lower end of the transect ("meadow soil") and soil from bare ground at the upper end of the transect ("bare soil"). In each following June (2010-2012), we thoroughly mixed all of each species' seeds before sowing them in potting soil at the University of Washington Botany Greenhouse. In July, after the seeds germinated, we randomly transferred the seedlings to individual containers that we filled with either meadow or bare soil.

In late August and early September, we planted these seedlings in the six study sites along the elevational transect. Within each site, there were ten plots, with half the plots located on a ridge and half in a nearby depression in the landscape. Thus, the plots experienced a wide range of microclimate conditions due to the differences in elevation and topographic position (ridge versus depression) (Ford et al. 2013). We measured the microclimate of the plots using temperature data loggers (HOBO Pendants made by the Onset Computer Corporation and iButtons made by Maxim Integrated Products) installed 3 cm below the soil surface adjacent to each plot that recorded soil temperature every two hours throughout the year.

Each plot received ten seedlings per focal species (though not every species was planted in every plot in every year due to the availability of seeds in the previous year – Appendix A). Seedlings were planted in cylinder-shaped holes (dug with a bulb planter) that were 10 cm deep and 5 cm in diameter. For each of the focal species, half of the seedlings in each plot were planted in holes filled with meadow soil and half were planted in holes filled with bare soil, corresponding to the type of soil in the seedling's container. After planting, we measured initial seedling size. The particular size attribute we measured differed by species depending on seedling morphology (Appendix A). Seedlings were well watered until the first substantial rain event in order to avoid mortality due to transplant shock. In each subsequent September (2011-2013), we resurveyed each seedling, noted whether it had survived and measured the size of each surviving seedling (the component of size we measured depended on the species' seedling morphology – Appendix A).

Data analysis

Calculating microclimate variables

We used the bihourly soil temperature recordings at each seedling transplant plot to calculate several microclimate variables that were potentially important for seedling establishment for each year at each plot. First, we estimated snow disappearance date (in the spring / summer) and annual snow cover duration. We could assess snow cover from the soil temperature recordings because snow insulates soil from fluctuations in air temperature so that temperatures beneath the snowpack in this region remain constant around 0ºC. Thus, the soil temperature data allowed us to determine whether snow was covering the plot for each day using an algorithm that considers daily temperature ranges and maxima (Lundquist and Lott 2008, Raleigh et al. 2013). We also estimated average daily mean, minimum and maximum soil temperature for all the days the plot was not covered by snow. Finally, we calculated growing degree days, which we defined as the annual sum of daily mean soil temperatures for all days with mean temperatures above 5°C (which all occurred during the snow-free period).

Modeling seedling survival and size

We fit all seedling survival and size models in a hierarchical Bayesian framework using Markov chain Monte Carlo (MCMC) simulation techniques (Gelman and Hill 2007). The microclimate variables were strongly correlated with each other (Appendix B). Thus, we decided to use one microclimate variable in our models of seedling survival and size. To decide which microclimate variable to use, we fit candidate models of survival and size for all seedlings that included one of the microclimate variables, soil type and the interaction of microclimate and soil as explanatory variables, and species identity as a random effect. We also included survey year as a categorical covariate and study plot as a random effect. We then calculated the deviance of each model. For both survival and size, the candidate model with snow disappearance date as the microclimate explanatory variable had the lowest deviance, suggesting it had the best fit. Thus, we used snow disappearance date, but no other microclimate variables, in all subsequent models.

We fit survival and size models separately for each species, as well as for seedlings of different ages (1-3 years olds). We fit two kinds of survival models for 2-3 year olds: an annual model, which estimated the probability of a seedling surviving to its current age conditional on it being alive the previous year, and a cumulative model, which estimated the unconditional probability of a seedling surviving to its current age. Both types of survival models had a Bernoulli error distribution. We fit models for the size of surviving seedlings using a Gamma error distribution. For both survival and size models, we included snow disappearance date (averaged over all years of a seedlings life for individuals greater than 1 year old for the cumulative survival and size models), soil type (meadow or bare) and their interaction as explantory variables, survey year as a categorical covariate (for species by age combinations with more than one year of data) and study plot as a random effect. To ensure adequate sample sizes, we excluded species by age combinations with fewer than 30 individual seedlings. This affected the analyses for 3 year olds from *Saxifraga tolmiei* and *Lupinus lepidus*. We then used the posterior distributions to derive expected mean values and 95% credible intervals for survival rates and sizes over the range of snow disappearance dates seedlings of each species experienced for both soil types.

All model fitting was implemented in JAGS using the rjags package (Plummer 2014) in R version 3.0.3 (R Core Team 2014). We assigned non-informative prior distributions to all parameters due to our lack of prior information, allowing the data to determine parameter estimation. For standard deviation parameters, we assigned uniform distributions on the interval

0-100. For intercepts and coefficients, we assigned a flat normal prior distribution with a mean of 0 and a variance of 1000. We ran the models with three MCMC chains and a burn-in of 20,000 iterations, and continued each MCMC run for 100,000 more iterations. The final 100,000 iterations were thinned to sample one out of every 100 iterations, yielding 3,000 iterations in total which we used to obtain posterior distributions for each parameter.

Results

First year survival was generally lower where snow disappeared earlier in the year, but this decrease in initial survival was often less severe and less significant for seedlings in meadow soil compared to bare soil (Figure 2). After the first year, snow disappearance date and soil had little effect on survival (Appendix C). However, for the tree species (*Abies lasiocarpa*), annual survival for 2 year olds in meadow soil was higher where snow disappeared earlier, which led to higher cumulative survival to age 2 and potentially age 3, but with only marginal significance (Figure 3).

The size of surviving seedlings at the end of the study was generally greater where snow disappeared earlier, but only in meadow soil (Figure 4). This interaction between snow disappearance and soil also resulted in seedlings in meadow and bare soil being about equally sized where soil disappeared late, but seedlings in meadow soil being substantially and significantly larger where soil disappeared early. However, this pattern did not hold for two of the seven focal species: the alpine forb *Saxifraga tolmiei* and the alpine nitrogen-fixing forb *Lupinus lepidus*. In these species, neither snow disappearance nor soil had a significant effect on seedling size.

Discussion

Climate and soil had important and interacting effects on seedling establishment that suggest climate change will lead to complex range shift dynamics in these mountain biomes. With climate change, snow disappearance is likely occur earlier in the year, and earlier snow disappearance had strong but surprisingly opposite impacts on seedling survival and size. However, soil type interacted with snow disappearance in such a way that meadow soil (found at lower elevations) will likely minimize the negative impacts of earlier snow disappearance on survival while magnifying the positive impacts on growth, relative to bare soil (found at higher elevations). And while snow disappearance and soil type had generally consistent effects on our seven focal species, the effects were much clearer for the lower elevation tree and subalpine species than the higher elevation alpine species. Together, these results suggest that the meadow species, particularly those found in the subalpine meadows, will contract at their lower limits (as trees encroach) faster than they expand at their upper limit, possibly leading to reductions in the geographic extent of the meadows (Figure 1, H_2). Below, we discuss specific results and how they lead us to these conclusions in more detail.

Interacting effects of climate and soil on seedling survival

For first year seedlings, water stress likely led to the reduction in survival with earlier snow disappearance (Figure 2), though the greater water holding capacity of meadow soils seems to alleviate the stress to some degree. The apparent importance of water stress was somewhat surprising because previous research has found that plant performance is generally energy-limited in this system (Stephenson 1990, Körner and Paulsen 2004, Albright and Peterson 2013). However, this region experiences little precipitation in the summer, despite receiving large amounts the rest of the year (Mass 2008), so there are few water sources for plants once the snowmelt is gone. These results are also consistent with findings in the nearby Olympic Mountains that seedling survival is negatively affected by low soil moisture levels (Soll 1994). Thus, as snowpacks disappear earlier in the summer, seedlings are more likely to experience water stress later in the growing season. Young seedlings are also likely to be particularly vulnerable to water stress because they tend to have poorly developed root systems (Harper 1977, Niinemets 2010). Meadow soils likely buffer these vulnerable seedlings from water stress due to their higher organic matter content which confers greater water holding capacity relative to bare soils (Appendix D).

However, our results also suggest that the negative impact of earlier snow disappearance on survival disappeared after the seedling’s first year. For older seedlings, earlier snow disappearance did not bring lower survival (Appendix C), suggesting that water stress was not particularly severe, likely due to these seedlings having more developed root systems. In fact, for the tree species (*Abies lasiocarpa*) it appears that the effect of earlier snow disappearance on cumulative survival becomes positive with marginal significance after the first year, but only in meadow soils (Figure 3). The combination of the older seedlings’ more developed root systems and the meadow soils’ higher water holding capacity may eliminate much of the water stress associated with earlier snow disappearance. At the same time, the combination of a longer growing season associated with earlier snow disappearance and higher concentrations of key nutrients (particularly nitrogen) associated with meadow soils may allow for enhanced resource capture that could lead to higher survival.

Interacting effects of climate and soil on seedling growth

Earlier snow disappearance generally led to greater size for seedlings in meadow soil but had no effect on size in bare soils (Figure 4), suggesting that a longer growing season improves growth but only when seedlings are in adequately high quality soil. Meadow soil is likely to be better for plant growth than bare soil for several reasons. One is the higher water holding capacity that helps ensure adequate soil moisture levels (Appendix D). A second is higher levels of nitrogen, because plant growth tends to be strongly nitrogen limited in these systems (Bowman et al. 1993, Heer and Körner 2002, Soudzilovskaia et al. 2005, Bassin et al. 2012). A third is higher concentrations of beneficial soil microbes, such as mycorrhizal fungi (Jumpponen et al. 2012). And while soils that developed in the presence of conspecific individuals can also have negative effects on plant growth due to factors such as increased pathogen levels (Bever 1994, Klironomos 2002, Kulmatiski et al. 2008), these impacts appear to be relatively minor in this system. The two species for which neither snow disappearance date nor soil type affected size (*Saxifraga tolmiei* and *Lupinus lepidus*) are both alpine plants common in locations with long-lasting snowpacks and poorly developed soil. To persist in such harsh environments, these species may have evolved life history strategies in which captured resources tend to be conserved rather than rapidly allocated to biomass production, so that short-term growth rates do not noticeably increase in more benign conditions (Grime 1979).

Implications for climate change and range shifts

The interactive effects of climate and soil on seedling establishment that we observed suggest that variation in soil characteristics across elevation will strongly modify seedling responses to climate change along this gradient. In lower elevation meadows, earlier snow disappearance brought by climate change will probably lead to increased seedling establishment because the negative effects of earlier snow disappearance on first year survival were relatively minor and often non-significant in meadow soil (Figure 2) while the positive effects on size tended to be substantial and significant (Figure 4). On bare ground at higher elevation, on the other hand, climate change may do relatively little to enhance seedling establishment. In these soils, earlier snow disappearance had negative effects on first year survival that were often strongly significant (Figure 2) while having no effect on size (Figure 4).

These patterns in seedling establishment suggest that plant species range shifts in response to climate change will be complex and lead to dynamics different from what would be expected if considering climate alone. For trees, upward range shifts into meadows will likely be relatively rapid because seedlings would be establishing in meadow soils. This expectation is consistent with observations of widespread tree establishment in subalpine meadows at Mount Rainier (Rochefort and Peterson 1996, Franklin et al. 1971) and the upward movement of treelines in many parts of the world (Harsch et al. 2009) in the last century. This tree encroachment will, in all likelihood, lead to declines in the shade-intolerant meadow plant species that cannot survive under tree canopies (Henderson 1974). In contrast, upward range shifts for many meadow plants, will likely be relatively slow because seedlings would be establishing in bare soils. This expectation is consistent with observations of primary succession at nearby Mount St. Helens, where plants have been slow to colonize bare ground following the 1980 eruption (del Moral et al. 2010). Thus, the ranges of meadow plant species, and the meadows as a whole, may contract at their lower limits faster than they expand at their upper limits, leading to an overall reduction in the geographic extent of their ranges (Figure 1, H_2).

This reduction in the land area of the meadows would pose a serious threat to biodiversity. Subalpine and alpine flora form a unique assemblage of species and many are only found in these habitats (Körner 2002), so reductions in the abundance of the habitat could result in the loss of numerous species. The asymmetric rates of range contraction and expansion will also likely exacerbate the stresses brought by subalpine and alpine climate regimes becoming more rare, due to upward shifts in climate regimes and there being less land at higher elevations (Thuiller et al. 2005, Rehfeldt et al. 2006, Engler et al. 2011). In all, these results highlight the importance of plant colonization and soil development on high elevation bare ground. Only a few subalpine or alpine species may be capable of driving these processes and developing the soil and habitat needed by many other species (del Moral and Wood 1993), making their range shift dynamics critically important for biodiversity in these biomes during the period of rapid climate change expected for the coming decades.

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Tables

Table 1. Focal species descriptions. The "Vegetation zone" column gives the vegetation zone the species is most abundant in.

Species	**Family**	**Vegetation zone**	**Functional group**
Saxifraga tolmiei Torr. & A. Gray	Saxifragaceae	Alpine	Forb
Lupinus lepidus Douglas ex Lindl. var. *lobbii* (A. Gray ex S. Watson) C.L. Hitchc.	Fabaceae	Alpine	Nitrogen-fixing forb
Carex nigricans C.A. Mey.	Cyperaceae	Alpine	Graminoid
Anemone occidentalis S. Watson	Ranunculaceae	Subalpine	Forb
Lupinus arcticus S. Watson ssp. *subalpinus* (Piper & Robinson) D.B. Dunn	Fabaceae	Subalpine	Nitrogen-fixing forb
Carex spectabilis Dewey	Cyperaceae	Subalpine	Graminoid
Abies lasiocarpa (Hook.) Nutt. var. *lasiocarpa*	Pinaceae	Subalpine	Tree

Figures

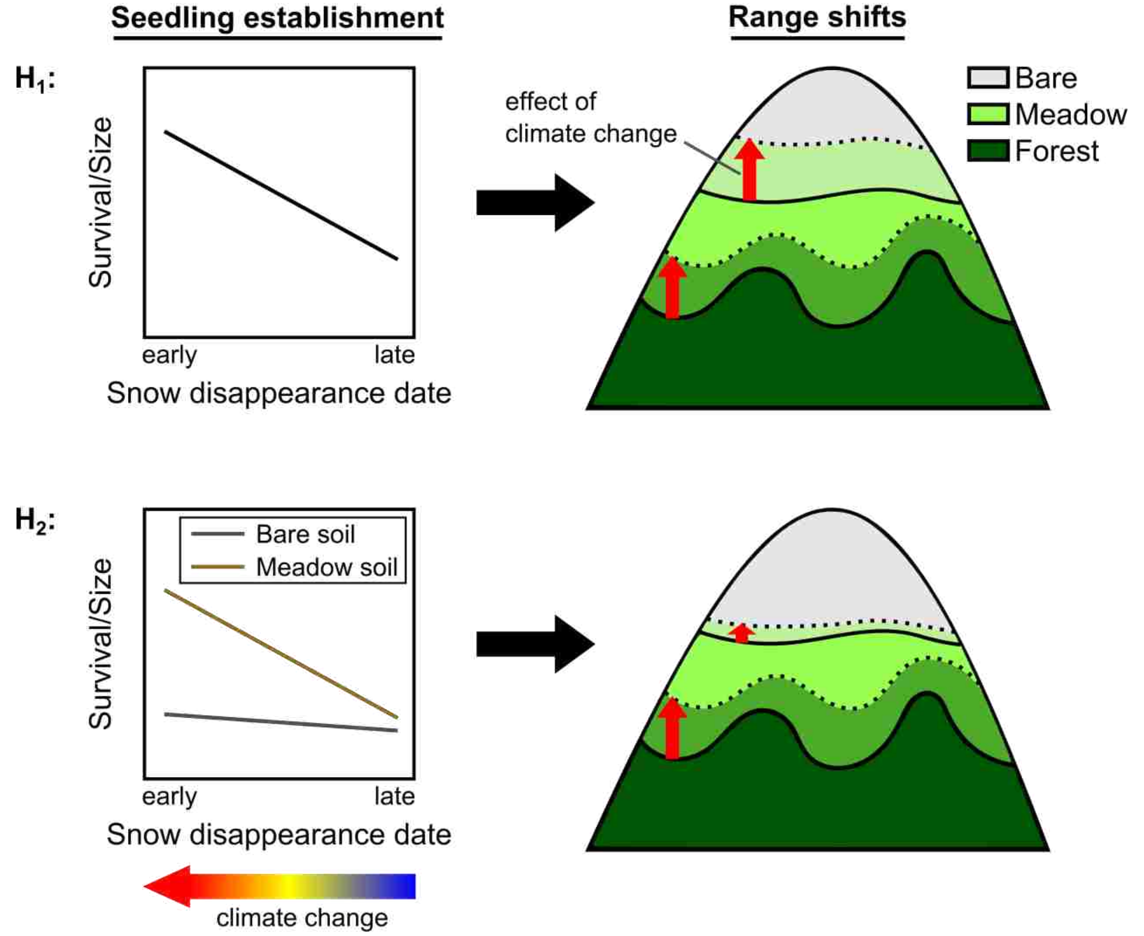

Figure 1. Schematic of potential seedling establishment patterns and their implications for climate-change-induced range shifts. H$_1$) Typical hypothesis for seedling establishment and range shift dynamics in mountain biomes when only considering climate. H$_2$) Hypothesis when considering climate and soil constraints on seedlings. See text for details.

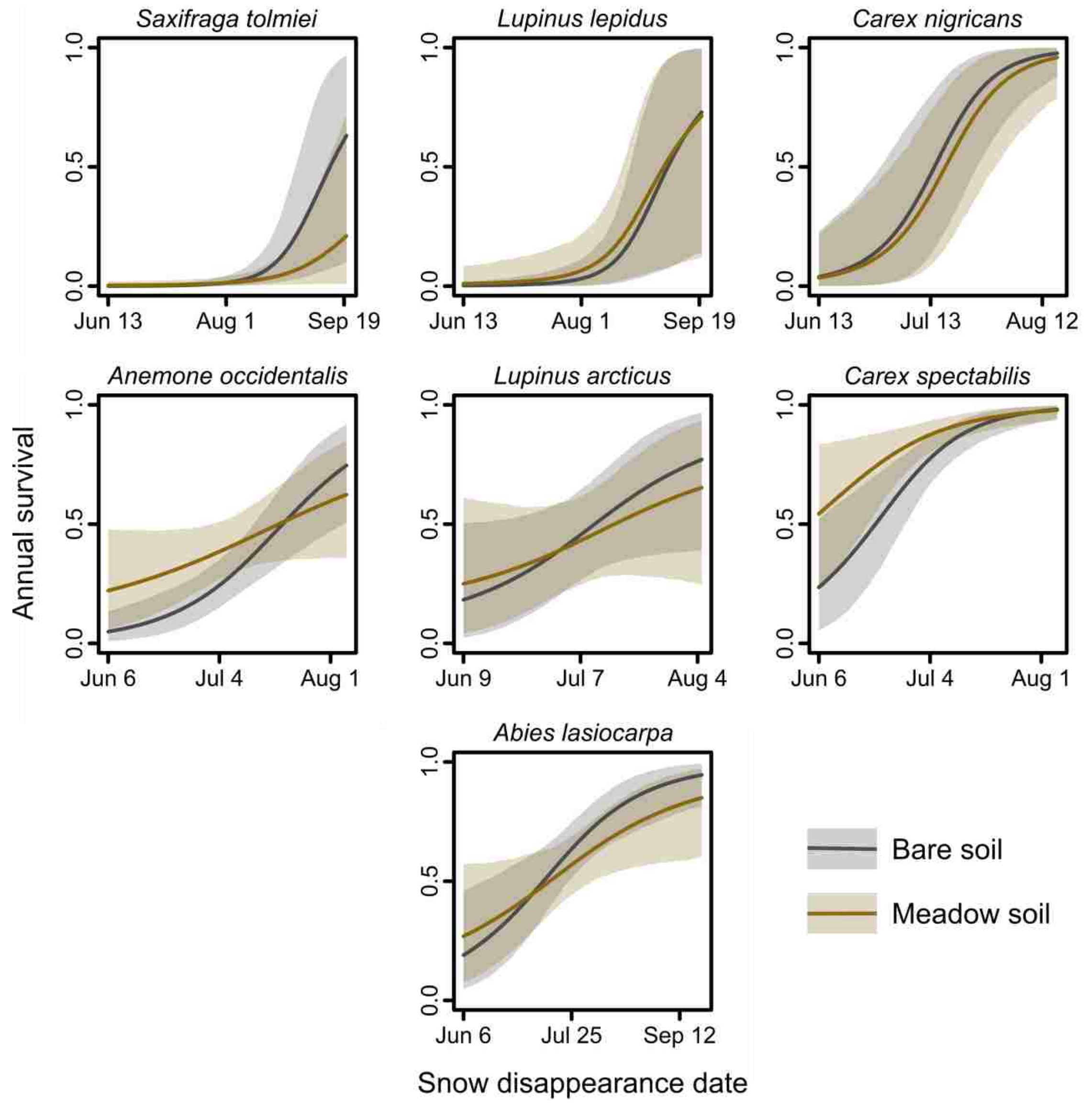

Figure 2. Annual survival rate for first year seedlings for different microclimate and soil conditions. Lines show the expected mean survival rate and shading shows the 95% credible intervals across the range of snow disappearance dates observed for the given species in the two soil types.

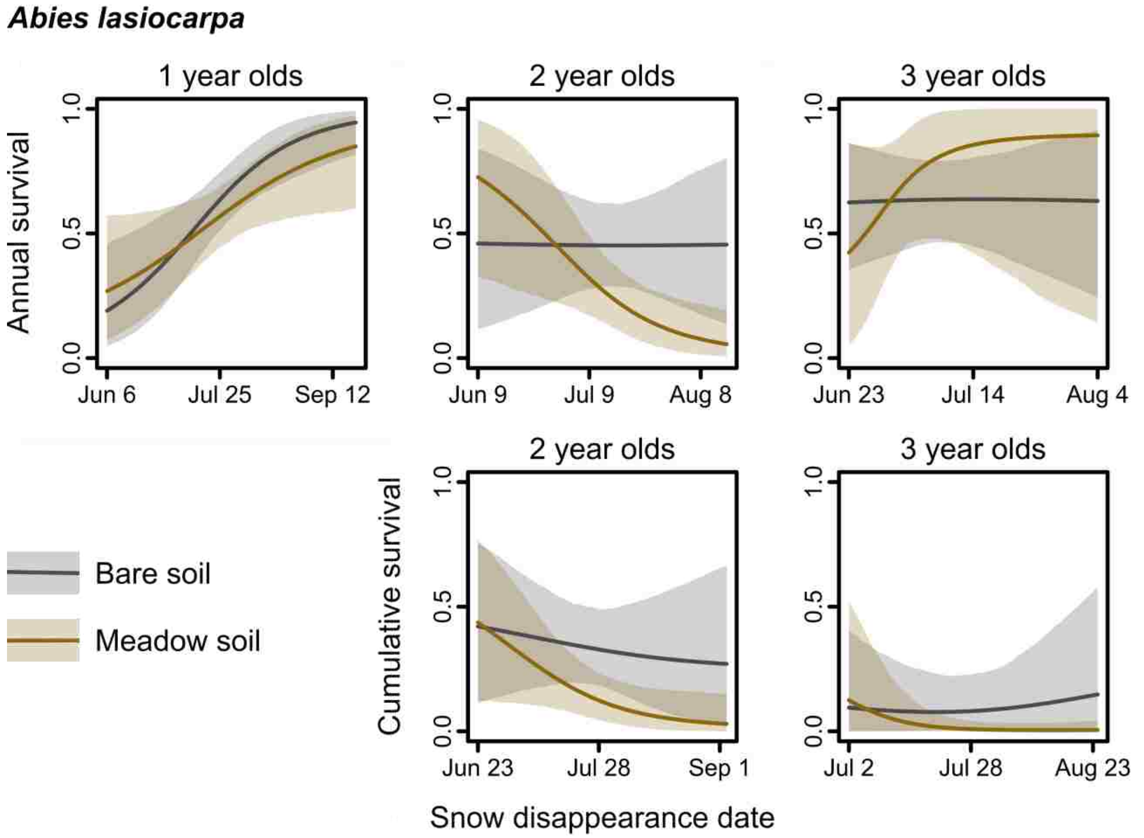

Figure 3. Annual and cumulative survival rates for 1, 2 and 3 year old *Abies lasiocarpa* seedlings for different microclimate and soil conditions. Lines show the expected mean survival rate and shading shows the 95% credible intervals across the range of snow disappearance dates observed for the given species in the two soil types.

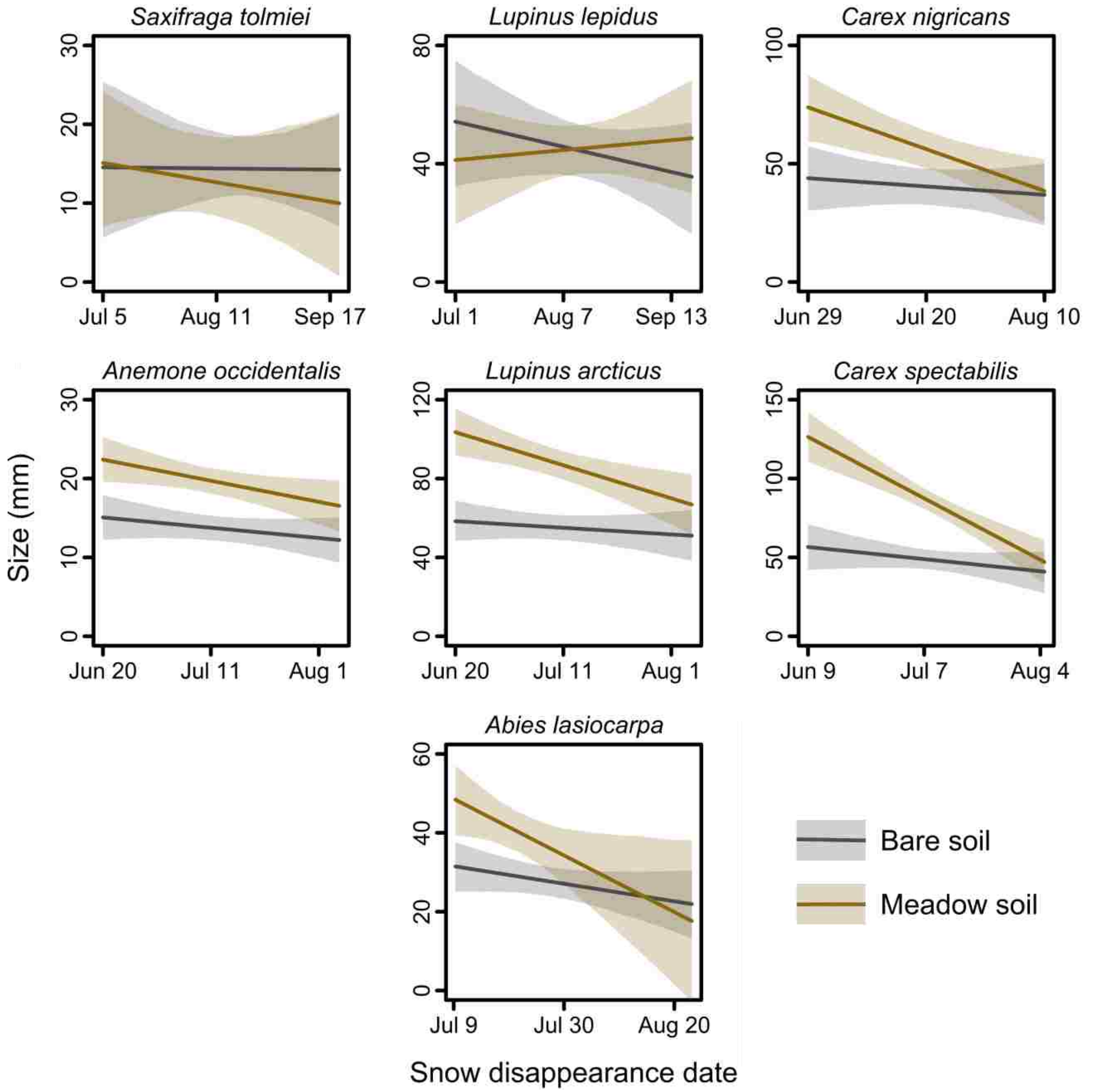

Figure 4. Size of surviving seedlings for different microclimate and soil conditions. Lines show the expected mean value for seedling size at the end of the study and shading shows the 95% credible intervals across the range of snow disappearance dates observed for the given species in the two soil types.

Supporting information

Appendix A. Study information

Table A1. Experimental design details.

Species	**Years seedlings were planted**	**Years seedlings were censused**	**Ages with sufficient sample sizes (>30 seedlings)**	**Size variable used**
Saxifraga tolmiei	2010, 2011	2011, 2012, 2013	1, 2 year olds	Total stem length
Lupinus lepidus	2010, 2011	2011, 2012, 2013	1, 2 year olds	Plant diameter – greatest horizontal distance between above ground plant parts
Carex nigricans	2011	2012, 2013	1, 2 year olds	Longest leaf length
Anemone occidentalis	2012	2013	1 year olds	Largest leaf diameter – greatest horizontal distance between parts of the leaf
Lupinus arcticus	2012	2013	1 year olds	Plant diameter – greatest horizontal distance between above ground plant parts
Carex spectabilis	2012	2013	1 year olds	Longest leaf length
Abies lasiocarpa	2010, 2011, 2012	2011, 2012, 2013	1, 2, 3 year olds	Total stem length

Appendix B. Correlations amongst microclimate variables

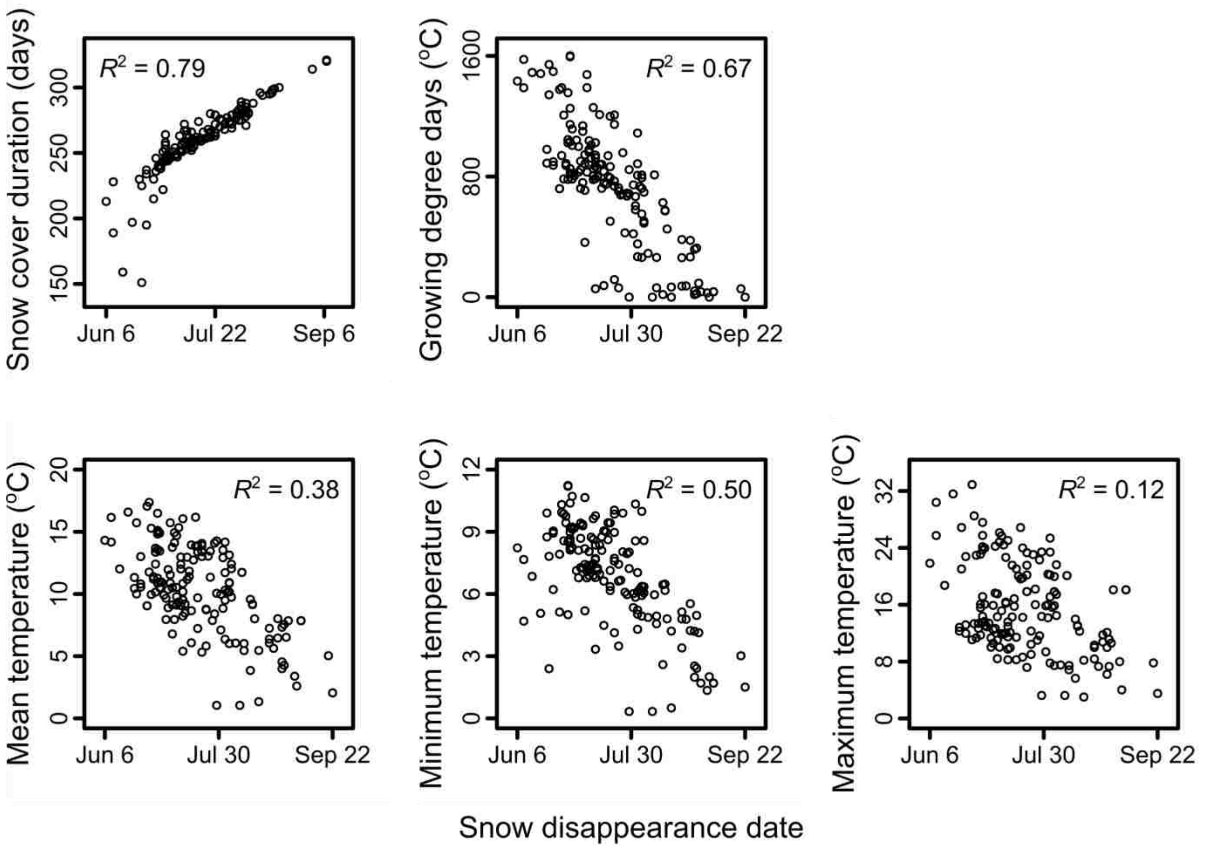

Figure B1. Correlations amongst microclimate variables. Scatterplots show the relationship between snow disappearance date and each of the other microclimate variables.

Appendix C. Seedling survival rates

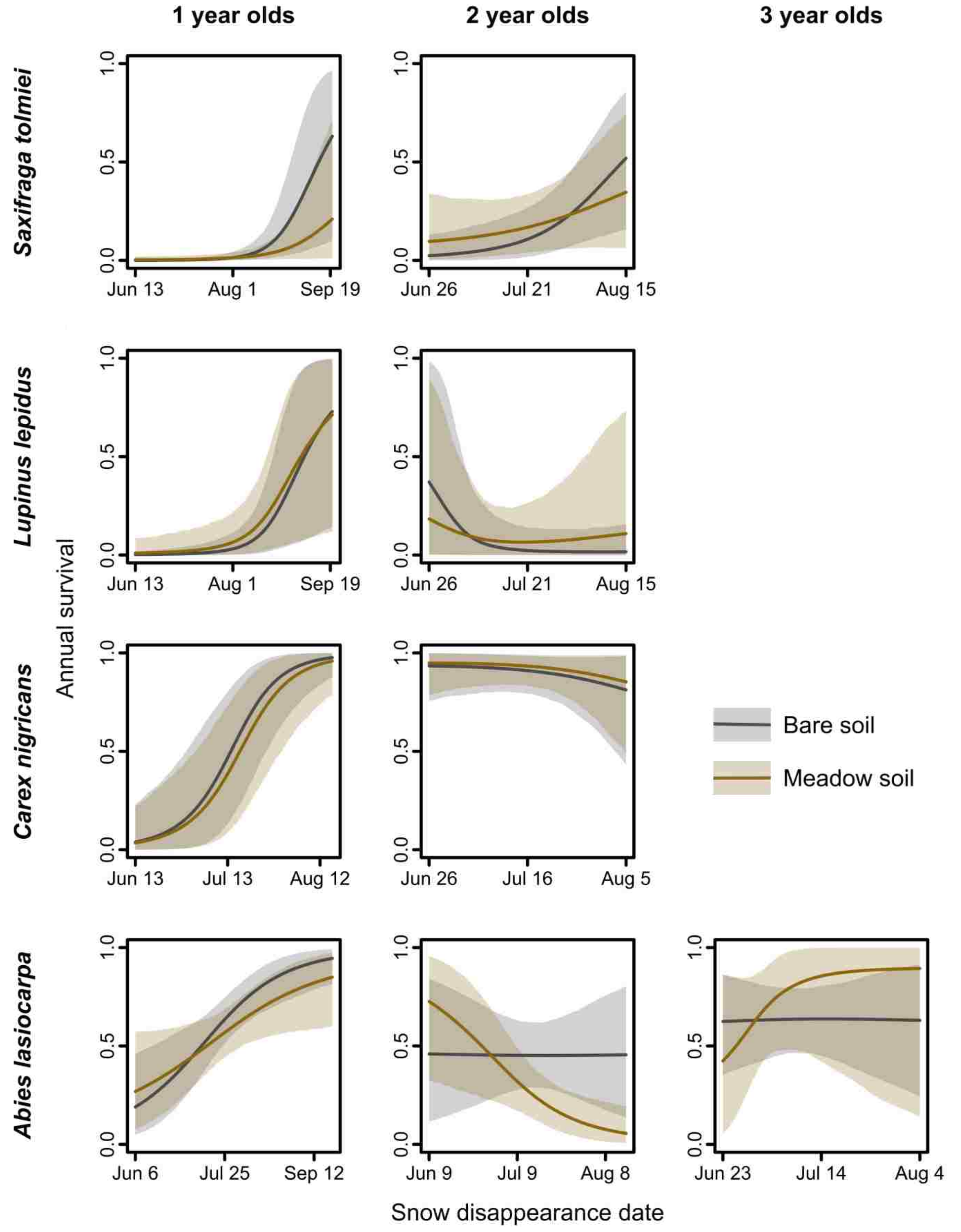

Figure C1. Annual survival rates of all seedling ages for focal species with multiple ages. Lines show the expected mean survival rate and shading shows the 95% credible intervals across the range of snow disappearance dates observed for the given species in the two soil types.

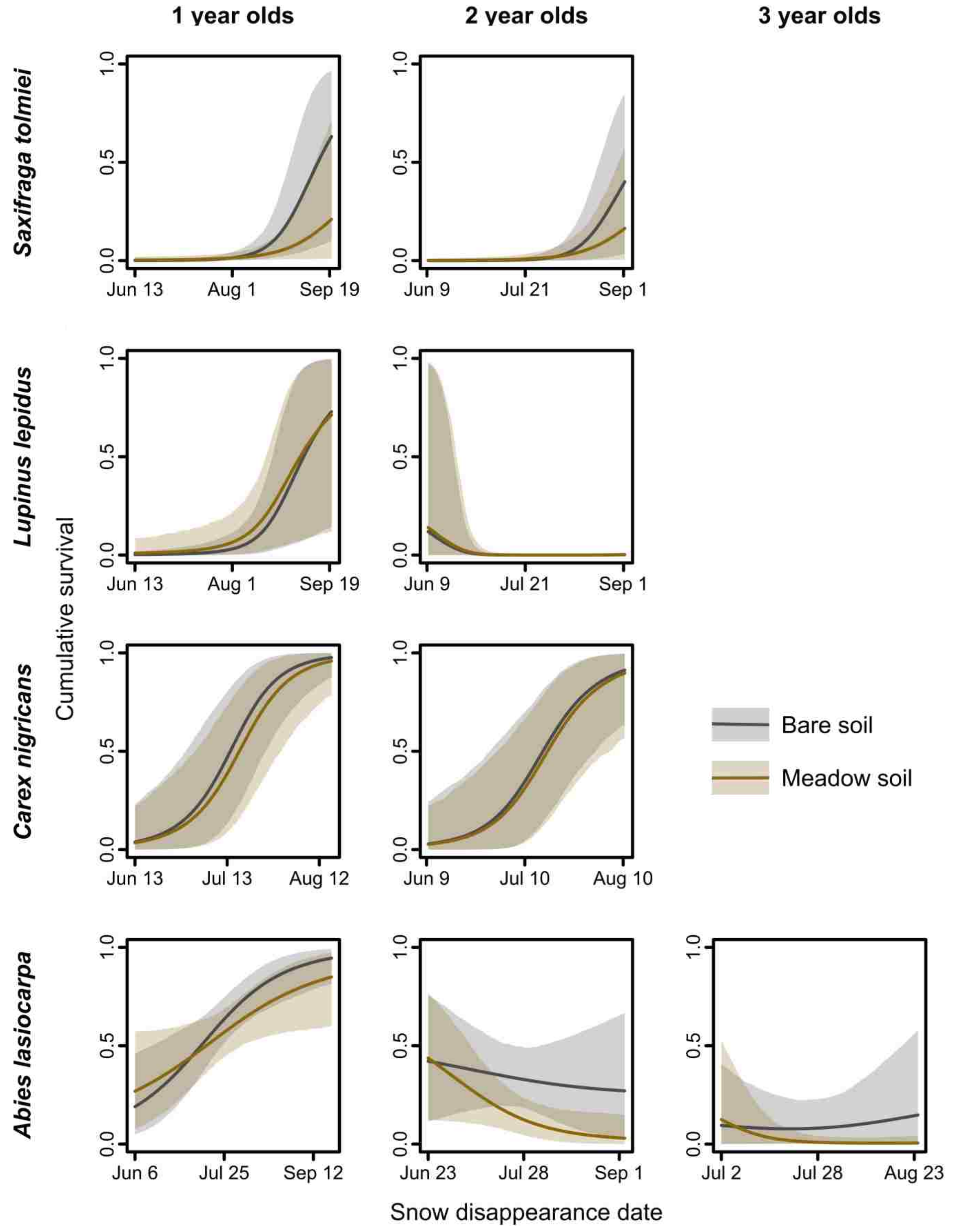

Figure C2. Cumulative survival rates of all seedling ages for focal species with multiple ages. Lines show the expected mean survival rate and shading shows the 95% credible intervals across the range of snow disappearance dates observed for the given species in the two soil types.

Appendix D. Soil characteristics across elevation

To characterize spatial patterns in soil organic matter content and water holding capacity across our study's elevational gradient, we collected soil samples from seven plots along an elevation transect spanning the subalpine and alpine meadows on the south side of Mount Rainer. Within each plot, we sampled from six locations differing in topographic position – two ridges, two depressions and two slopes – for a total of 42 samples for both the organic matter content and water holding capacity tests.

To calculate soil organic matter content (the proportion of organic material in the soil), we first dried the sample to remove all moisture, recorded the mass of the dry soil, placed the dried soil in a muffle furnace set to 400°C for 10 hours to volatilize all organic matter and then recorded the mass of the remaining unburned soil. We subtracted the mass of the unburned soil from the mass of the dried soil to obtain the mass of the organic matter in the sample. We then calculated organic matter content as the mass of organic matter in the sample divided by the mass of the dried soil sample.

To calculate soil water holding capacity, we dried each sample to remove all moisture, recorded the mass of the dry soil, saturated the soil with water and then recorded the mass of the wet soil. We subtracted the mass of the dry soil from the mass of the wet soil to obtain the mass of the water held by the soil. We then calculated soil water holding capacity as the mass of the water held by the soil divided by the mass of the dry soil.

We used generalized linear models to test the importance of elevation, topographic position and their interaction on organic matter content (Beta error distribution) and soil water holding capacity (Gamma error distribution). The best-fit model for both soil variables included elevation but not topographic position or the interaction of elevation and topographic position (based on AIC – Akaike's Information Criterion). To assess the significance of pairwise differences in organic matter content and soil water holding capacity amongst elevations, we performed multiple comparison tests in R version 2.12.0 (R Development Core Team 2010) using the multcomp package (Hothorn et al. 2008). Both organic matter content and soil water holding capacity are lower at higher elevations and seem to cross a threshold around 1900 m, the upper limit of the subalpine/alpine meadows (Figure D1). Below 1900 m the ground is mostly covered in vegetation, while above 1900 m it is mostly bare.

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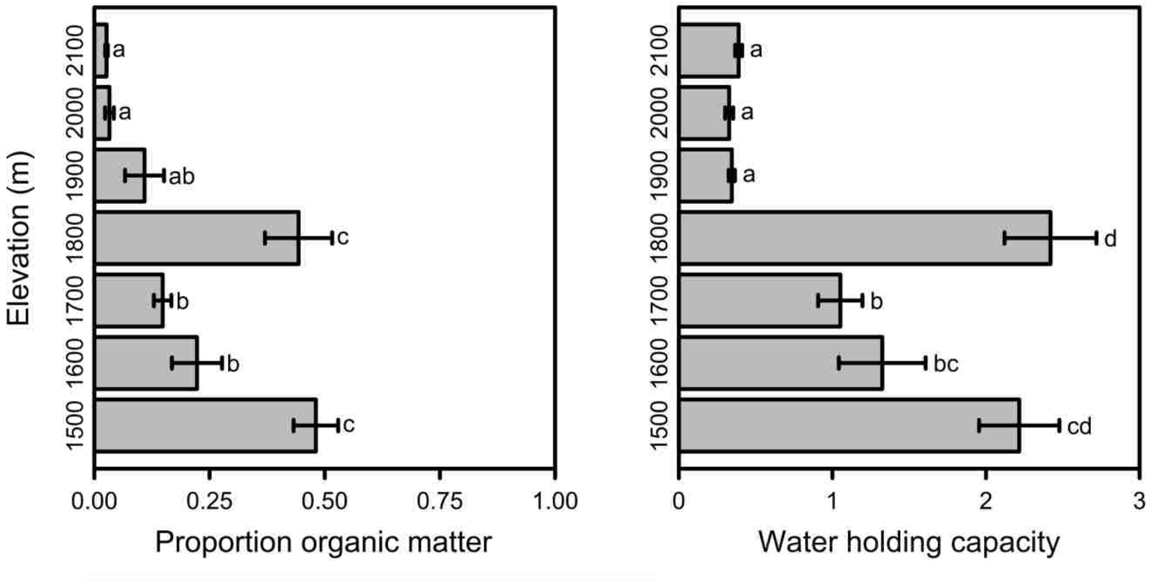

Figure D1. Mean soil characteristics across elevation. Bars with same letter are not significantly different (multiple comparison test, α=.05). Error bars show standard error.

Chapter 4: Growth patterns across tree species elevational ranges suggest complex impacts of climate change

Kevin R. Ford, Ian K. Breckheimer, Jerry F. Franklin, James A. Freund, Steve J. Kroiss, Andrew J. Larson, Elinore J. Theobald, Janneke Hille Ris Lambers

Abstract

Tree growth strongly influences the population dynamics of tree species and the functioning of forest ecosystems. To anticipate how forests will respond to future climate change, it is therefore critical to understand how climate influences tree growth. Trees can differ greatly in their responses to climate based on their size, making it important to also understand how climate-growth relationships vary with individual size. We addressed these issues by studying size-growth relationships across a large elevational/climatic gradient for four dominant Pacific Northwest tree species (*Abies amabilis*, *Tsuga heterophylla*, *Pseudotsuga menziesii* and *Thuja plicata*). Our data were drawn from a large forest inventory dataset, with 6,783 individuals tracked from 1976-2008 in fifteen 1 ha plots spanning 900 m of elevation at Mount Rainier National Park, Washington State, USA. Mean growth of three of the four focal species declined from low to high elevations, implying that growth is generally constrained by cool and short growing seasons at higher elevations. The other species, *Pseudotsuga menziesii,* showed no trend in growth across elevation, possibly because it is a shade-intolerant pioneer species and thus more responsive to fine-scale differences in light environment in these closed canopy forests than coarse-scale differences in climate across its elevational range. For the species that did exhibit a growth trend across elevation, species differed in the size class most responsible for growth reductions at high elevations. For *Abies amabilis* and *Tsuga heterophylla,* small trees

exhibited greater declines in growth with increasing elevation than large trees, while the opposite was true for *Thuja plicata*. Our results suggest that at upper range margins, warming will relieve constraints on growth and lead to higher productivity and population density for many, but not all, tree species. Additionally, the rate and extent to which warming-induced increases in individual growth translate to increased population-wide density and productivity may vary among species, because growth and the sensitivity of population and ecosystem dynamics to growth depend on individual size. These species- and size-specific patterns in growth across elevation imply that species will respond to climate change individualistically, potentially leading to forest communities different than ones observed today.

Introduction

Understanding the connections between climate and tree growth is essential to understanding how the functioning and biodiversity of forest ecosystems will respond to climate change. Individual tree growth plays a key role in determining forest structure and function, both directly through physiological processes (e.g., photosynthesis, biomass production) and indirectly through the influence of growth on survival and population dynamics (Monserud 1976, Wyckoff and Clark 2002, Moorcroft et al. 2001). Forests account for half of all terrestrial carbon stocks and net primary production (Sabine et al. 2004) and two thirds of terrestrial biodiversity (Millennium Ecosystem Assessment 2005), so climate-change-induced alterations to the ecosystem services forests provide could have substantial global consequences (Bonan 2008).

One approach for studying the relationship between climate and tree growth is to measure growth across large elevational gradients. This approach allows ecologists to explore the complexities of species responses to differences in climate by observing growth rates across a wide range of climatic conditions in natural populations. For example, growth may not always decrease from species range cores, where organisms presumably experience optimal climatic conditions, to range margins (Loehle 1998, Coomes and Allen 2007, Purves 2009, Rapp et al. 2012) as is generally assumed (Sexton et al. 2009). Instead, different species may exhibit a variety of trends in growth across their ranges (Figure 1A). Such species-specific differences in climate-growth relationships would imply that species will respond to climate change individualistically, which could lead to the formation of communities with novel composition and structure.

Furthermore, not all individuals within a species may respond in the same way to differences in climate, which can influence how species and ecosystems respond to climate change. Specifically, individual size can strongly affect whether and how trees respond to differences in the environment (Easdale et al. 2012) (Figure 1B). Size-specific differences in sensitivity to climate within and between species matter because they can govern the rate at which populations of long-lived trees respond to climate change. For example, because the success and establishment of new trees drives range expansions, more rapid upward expansions would presumably occur if warming increases the growth of small (young) individuals at a species' upper-elevational limit. By contrast, if warming only increases the growth of large (old) trees at their upper limit, range expansions might be slow (Figure 1B). Size-specific differences in the sensitivity of growth to climate can also influence the response of ecosystem functioning to climate change. For example, larger trees typically have higher growth rates, and thus disproportionately influence productivity, carbon fluxes and other ecosystem processes. Therefore, the effects of climate change on the growth of larger trees will likely have a disproportionately strong influence on ecosystem dynamics (Stephenson et al. 2014). Thus, it is important to understand how size influences climate-growth relationships.

To address these issues, we quantified the growth rates of four dominant Pacific Northwest forest tree species (*Abies amabilis*, *Tsuga heterophylla*, *Pseudotsuga menziesii* and *Thuja plicata*) across a large elevational/climatic gradient at Mount Rainier National Park using a large and long-term forest inventory dataset. These types of datasets have become much more widely available in recent years and provide opportunities to gain new insight into potential responses of tree species and forests to climate change. We addressed three main questions: 1) How does mean tree growth vary across the elevational range of a species (integrating across individuals of different sizes)? 2) How does growth vary with individual tree size? 3) How does the elevation-growth relationship differ amongst individuals of different sizes?

We hypothesized that 1) growth would be highest in the core of species elevational ranges and decline towards range margins (Figure 1A – H_1), but that there would be variability amongst species. We also hypothesized that 2) growth would increase with size because larger trees have greater leaf and root biomass that leads to greater resource capture and absolute growth. But, we expected the rate of increase with size to decline with increasing size because larger trees have a higher proportion of non-photosynthetic biomass, greater self-shading of leaves and more depleted local soil nutrient concentrations, which would lead to lower growth relative to size (Weiner and Thomas 2001, Paine et al. 2012). Finally, we expected *that 3)* elevation-growth patterns would be less pronounced for smaller individuals, because small trees in the understory are more limited by light availability than larger trees with higher canopies which would be more sensitive to climate differences across elevation (Figure 1B – H_1).

Methods

Study system

Mount Rainier National Park occupies a mountainous landscape with steep climatic gradients, encompassing 95,354 ha of the western Cascade Mountains in Washington State, USA. Forests dominate at lower elevations and constitute 60% of the Park's land area. The region experiences a temperate, maritime climate with mild, dry summers and cool, wet winters. Temperature decreases and precipition increases with elevation, leading to larger and longer lasting snowpacks at higher elevations (Figure 2). The distributions of tree species at Mount Rainier are strongly correlated with patterns in climate, namely temperature, precipitation and snowpack duration (Franklin et al. 1988). Mount Rainier's forests are notable for the abundance of old-growth stands and the presence of very large and old trees (Franklin et al. 1988).

Data collection

Fifteen permanent sample plots were established at Mount Rainier between 1976 and 1978 as part of the Pacific Northwest Forest Permanent Sample Plot Network. These plots span an elevational range of 595 – 1502 m (Figure 2, Appendix A). In each 1 ha plot, all trees with a diameter at breast height (DBH) value greater than 15 cm (and all trees greater than 5 cm DBH in four randomly selected 25x25 m subplots) were tagged and measured for DBH. The surviving trees and any new trees that grew to become larger than the minimum DBH threshold (5 or 15 cm – depending on the subplot) during the study have been re-measured roughly every 5 years, with the latest data collected in 2008 (Acker et al. 1998, Larson and Franklin 2010).

Focal species

We restricted our analyses to tree species that met the following criteria: 1) was present in plots that spanned an elevational range of at least 500 m, 2) had at least 15 individuals in a minimum of 6 plots, and 3) had a total of 100 individuals across all plots. Four of the 17 tree species in the plots met all selection criteria: *Abies amabilis* (Pinaceae), *Tsuga heterophylla* (Pinaceae), *Pseudotsuga menziesii* (Pinaceae) and *Thuja plicata* (Cupressaceae). There were 6,783 individuals of these focal species in the study, which represented 84% of all individuals across all plots. The local elevational range of *Abies amabilis* is mostly contained within the Park, with its upper range boundary extending to the treeline ecotone and few individuals found lower than the Park's valley bottoms. The upper limits of *Tsuga heterophylla*, *Pseudotsuga menziesii* and *Thuja plicata* are found within the closed-canopy forests of Mount Rainier, with their ranges extending past the lowest elevations of the Park and down to sea level in the region.

Data analysis

The overarching goal of these analyses was to characterize how growth varies over tree species elevational ranges and how these relationships vary for individuals of different sizes. We calculated tree size in terms of basal area – the area of land occupied by the tree's trunk – which we estimated from the DBH measurements. Mean annual growth rate was estimated as the amount of basal area the individual accrued over the time it was tracked in the study divided by the number of years it was tracked. We used tree size as an explanatory variable in the growth analyses and calculated it as the midpoint of the individual's basal area over the time it was tracked (see Appendix B for tree size distributions).

With these data, we built a nonlinear mixed effect model of tree growth for each focal species that included size and elevation as fixed effects and plot as a random effect (Zuur et al. 2009). To do this, we first fit a series of candidate models describing potential relationships between size and growth for a given species. The models included*:* 1) a null model in which growth was constant with respect to size, 2) a linear model, 3) an asymptotic model described by a monomolecular curve, and 4) a potentially hump-shaped model described by a Ricker curve (Appendix C). As a group, the candidate models provided the flexibility to model a variety of linear or nonlinear relationships that are commonly used for describing plant size-growth relationships (Paine et al. 2012), ranging from no relationship (model 1), to one that allows for senescence (model 4). For each species, we selected the best-fit model based on AIC_c (Akaike's Information Criterion with a correction for finite sample sizes) (Burnham and Anderson 2002).

We next tested whether and how these size-growth relationships varied across species elevational ranges. Specifically, after selecting the best-fit size-growth model for each species, we tested whether the values of the parameters describing the size-growth relationship varied with elevation. To do this, we created another series of candidate models in which each parameter of the best-fit size-growth model had one of three possible relationships with elevation: 1) a null relationship in which the parameter value was constant with respect to elevation, 2) a linear relationship (which could be positive or negative) and 3) a quadratic relationship (Appendix C). Candidate models for each species contained every possible combination of these relationships for each parameter of the best-fit size-growth function. These candidate models allowed for a wide variety of elevation-growth relationships for each species (flat, monotonic or humped shaped), and importantly, allowed these responses to differ by individual size. We used AIC_c to select the final best-fit elevation-size-growth model. All models were built using the nlme package (Pinheiro et al. 2012) in R (R Core Team 2012).

For each species we then calculated how mean growth for a population varies across that species' elevational range at Mount Rainier. We did this by calculating the expected mean growth rate (in cm^2 of basal area per year) for each species across the range of elevations it was observed in (at 10 m intervals) based on the best-fit growth model. Because the distribution of tree sizes also varied across elevation (Appendix D), we applied these models to the entire population of each species in the dataset (i.e., all individuals observed in all plots) at each elevation interval and calculated the mean of the expected growth rates, thus controlling for elevation-size relationships. This also allowed us to apply our model to a real population of trees with a representative distribution of individual sizes for each species. We used nonparametric bootstrap sampling to place confidence intervals around our estimates of expected mean growth rates across size (for all elevations) and across elevation (controlling for size) for each species (sampling 10,000 times with replacement).

To visualize how tree size modulates the relationship between elevation and growth in our models, we calculated expected growth across elevation for individuals of different size classes for each species in which there was a trend in mean growth across elevation. We did this by splitting up the population of each species into five size classes, with each size class covering the same range of sizes and together covering the entire range of sizes observed for that species in the plots. We also plotted the difference in growth relative to size between the lower and upper elevational margins in the study for each species across the observed range of sizes for that species.

Results

The nature and strength of the relationship between elevation and growth differed by species (Table 1, Figure 3). Elevation was included in the best-fit models for *Abies amabilis*, *Thuja plicata* and *Tsuga heterophylla*, but not *Pseudotsuga menziesii* (Table 1). For *Abies amabilis*, whose local elevational range is almost entirely contained within the study plots, growth declined monotonically with increasing elevation so that the highest growth rate was near the species' lower range margin (Figure 3). *Tsuga heterophylla* and *Thuja plicata* also experienced monotonic declines in growth with increasing elevation from the lowest plots at Mount Rainier (which are in the core of their elevational ranges) to their upper margins (Figure 3). For *Pseudotsuga menziesii*, growth did not vary with elevation across the species' range at Mount Rainier (Figure 3).

Size was a strong predictor of growth for all species, with the AIC_c of the best-fit size-growth models being much lower (more parsimonious) than the null models (Table 1). Growth increased with size, but at a decreasing rate, for *Abies amabilis, Pseudotsuga menziesii*, and *Thuja plicata* (Figure 4). Growth also increased with size for smaller *Tsuga heterophylla* individuals, but declined with size for larger individuals, resulting in a hump-shaped relationship between size and growth (Figure 4).

For the three species that did exhibit a correlation between elevation and mean growth, the magnitude of growth reductions with increasing elevation depended on size (Figure 5). For *Abies amabilis* and *Tsuga heterophylla*, small trees showed greater declines in growth with increasing elevation than large trees. We found the opposite pattern for *Thuja plicata*, with large trees showing greater declines in growth with increasing elevation (Figure 5).

Discussion

We found that individual tree growth generally declined from the core of a species range to its upper elevational range margin, but with important exceptions and nuances likely to influence the rate and magnitude of forest responses to climate change. First, growth did not decline at range margins in all cases, with one of the focal species (*Pseudotsuga menziesii*) showing no trend in growth across elevation, and another (*Abies amabilis*) showing its highest growth rate at its lower range margin. Second, size-growth relationships varied by elevation in a species-specific manner, implying that species will differ in whether small versus large trees will show the greatest response to climate change. Below, we speculate on the mechanisms behind these findings and their potential implications for forests during periods of climate change.

Growth varies by elevation

Reduced tree growth at high elevations (Figure 3) was likely due to stresses imposed by the cooler temperatures and longer periods of snow cover (i.e., shorter growing seasons) found at these locations (Figure 2) (e.g., Graumlich et al. 1989, Peterson and Peterson 1994, Littell et al. 2008, Ettinger et al. 2011), though there was variation amongst species in the magnitude of these growth reductions. The highest elevation species, *Abies amabilis*, showed the greatest decline in growth with increasing elevation, while the one pioneer species, *Pseudotsuga menziesii*, did not exhibit any trend in growth across elevation, possibly because it is relatively shade-intolerant (Minore 1979). In these closed-canopy forests, the growth of *Pseudotsuga menziesii* may be more sensitive to fine-scale differences in light environment within similar elevations than coarse-scale differences in climate or other factors across its elevational range at Mount Rainier (especially compared to the three other focal species which are very shade-tolerant). A study of tree seedling growth across elevation at Mount Rainier found that growth rates declined monotonically with increasing elevation (Ettinger and HilleRisLambers in prep), as we generally found in this study of adult individuals, suggesting that the patterns we observed could match those in smaller size classes than the ones we measured.

We did not find any evidence that growth was constrained at low elevations for the focal species whose lower range margin is found near the lowest plots at Mount Rainier (*Abies amabilis* – Figure 3), contrary to our expectation of declining performance at range margins (Fig 1A – H_1). It is possible that this species' lower range limit may instead be determined by competition with lower-elevation species (Loehle 1998) or by climatic effects on other vital rates, such as survival (Doak and Morris 2010). Our findings that growth was sensitive to broad-scale differences in the environment at species upper but not lower range margins are consistent with tree-ring based studies of growth at Mount Rainier, which found that growth was positively related to warmer temperatures, longer growing seasons and reduced snowpacks at high elevations, but that climate was a weak and inconsistent predictor at lower elevations (Ettinger et al. 2011, Ettinger and HilleRisLambers 2013).

Growth varies by individual size

The strong relationship we found between size and growth demonstrates the importance of including size as a covariate in tree growth studies. Growth increased with increasing size for small individuals, but the rate of increase either declined for medium to large individuals (*Abies amabilis*, *Pseudotsuga menziesii* and *Thuja plicata*) or growth reached a peak with medium-sized individuals (*Tsuga heterophylla*) (Figure 4). These size-growth relationships are generally consistent with two widely observed patterns: 1) absolute growth rates tend to increase with tree size (Stephenson et al. 2014, Sillett et al. 2010), likely due to larger trees having greater leaf and root biomass that leads to greater resource capture – see Appendix F for a comparison of our approach to the approach of Stephenson et al. (2014); and 2) relative growth rates tend to decline with size, likely because larger trees typically have a higher proportion of non-photosynthetic biomass, greater self-shading of leaves and more depleted local soil nutrient concentrations, which reduces growth given size (Paine et al. 2012, Ishii et al. 2000). And because size is an important predictor of growth, if size covaries with an explanatory variable of interest, such as elevation in this study, it can have a confounding effect on interpretations of the importance of that explanatory variable. For example, absolute growth rates for *Pseudotsuga menziesii* declined with increasing elevation in the study plots, but size also decreased with elevation (Appendix D). After accounting for the positive relationship between size and growth for this species (Figure 4), we found no consistent relationship between elevation and growth (Figure 3).

Growth varies across elevation in size-specific ways

Declines in growth with increasing elevation were driven by trends in different sized trees for different species, suggesting that distinct mechanisms may be responsible for the common pattern of decreasing mean growth towards species upper range margins. For *Thuja plicata*, large individuals showed the greatest reductions in growth with increasing elevation (Figure 5). In this species, possible reductions in photosynthesis at higher elevations due to lower temperatures and shorter growing seasons may be especially stressful for larger trees due to these individuals having smaller ratios of photosynthetic to non-photosynthetic tissues, and thus a greater dependence on high performance of the photosynthetic tissues to support the plant (Paine et al. 2012). For *Abies amabilis* and *Tsuga heterophylla*, on the other hand, small individuals showed the greatest declines in growth with increasing elevation (Figure 5). In these species, the mechanical stresses imposed by large snowpacks at high elevations (crushing, tearing, etc.) may be particularly damaging for small trees that have lower load-bearing capacities than larger trees (King 1991, King 1997). Large snowpacks can also lead to partial or complete burial of small trees late into the year, which can delay shoot elongation and shorten the growing season relative to larger trees (Grier et al. 1981).

Implications for responses to climate change

The size-specific elevation-growth relationships we observed can help us understand how species population densities, community structure and ecosystem processes in these forests might respond to climate change. For example, our results suggest that warming will likely lead to increased productivity and population density (in terms of basal area per unit land area) at the upper range margins for many tree species. At these locations, growth is currently depressed for most focal species (Figure 3), likely due to low temperatures, large snowpacks and short growing seasons. Warming will relieve these climatic stressors (Mote and Salathe 2010, Elsner et al. 2010), which could result in increased individual growth rates and higher population densities (Albright and Peterson 2013). However, responses will likely differ by species because the magnitude of growth declines varied by species. For instance, we might expect the population density response to be particularly strong for *Abies amabilis* because it showed the greatest reduction in growth at the upper range margin (Figure 3).

In contrast, at the lower range margin of *Abies amabilis* (the only focal species with upper and lower range limits near our study area) there was no evidence that warming will lead to a decline in tree growth because growth increased from the range core to the lower margin (Figure 3). If this result can be generalized to other species, then the declines in population densities that might be expected in the lower and middle portions of a species range with climate change could be slow as individuals maintain relatively high growth rates. Ultimately, declines in population density may depend on mortality rates (Larson and Franklin 2010, van Mantgem et al. 2009) and the rates at which warmer adapted tree species expand their ranges into these areas.

The size-specific patterns in tree growth across elevation also suggest that the rate at which populations respond to climate change will vary by species. For example, increases in population size at and above upper range limits might be especially fast for *Abies amabilis* and *Tsuga heterophylla*. For these species, the growth rates of small trees were most depressed at the upper range margin (Figure 5), and are thus likely to have the most potential to increase as low temperature and high snow stressors are relieved. Because these small trees establish new populations and drive range expansions, growth responses of these individuals may be most important for driving changes in the density of upward expanding populations as climate change progresses (Figure 1B – H_2). In contrast, population growth at and beyond the upper range limit of *Thuja plicata* may be slow because the growth rates of small trees were not depressed at these locations, suggesting that warming may have only minor impacts on the recruitment of small trees to larger size classes (Figure 5).

In all, the species-specific patterns in mean and size-specific growth across elevation suggest that climate-change-induced shifts in population densities will likely be complex and individualistic, and could lead to forest communities different from those found in this area today (Davis 1986). This phenomenon has been observed in the fossil record (e.g., Brubaker 1986, Kullman 1995, Davis and Shaw 2001, Gavin et al. 2001) and in recent decades (e.g., Moritz et al. 2008, le Roux and McGeoch 2008, Harsch et al. 2009, Chen et al. 2011), though an understanding of the demographic mechanisms behind these shifts in community structure is typically lacking, but can gained through studies such as this one.

The size-specific patterns in tree growth across elevation also imply that an explicit consideration of size is needed to realistically assess how forest ecosystem processes will respond to climate change. In Mount Rainier's forests, warming-induced increases in productivity may be relatively small because large individuals of the most dominant species (*Abies amabilis*, *Tsuga heterophylla* and *Pseudotsuga menziesii*, together representing 74% of total basal area in the study plots) exhibited little or no change in growth across the climatic gradient. These larger trees generally have higher growth rates, and thus disproportionately influence productivity and other ecosystem processes (Stephenson et al. 2014). In fact, the largest 50% of trees were responsible for 82-88% of total growth for the focal species. Although large individuals of one focal species (*Thuja plicata*) did show a steep decline in growth across elevation, this species represented just 13% of total basal area of the plots. In light of our study and others, it is clear that climate change will likely have important impacts on tree populations and forest ecosystems, but that responses will be irregular and complex.

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Tables

Table 1. Model results. The “size-growth relationship” column lists the curve that best described that relationship for the given species (Appendix C). The “$\Delta \mathrm{AIC}_c$ – size” column represents how much model fit is improved by incorporating size as an explanatory variable (compared to a null model with no explanatory variables), and is the AIC_c value of the null model minus the AIC_c value of the best-fit size-growth model. The “$\Delta \mathrm{AIC}_c$ – elevation” column represents how much model fit is further improved by incorporating elevation as an explanatory variable in addition to size, and is the AIC_c value of the best-fit size-growth model minus the AIC_c value of the best-fit elevation-size-growth model, or “0” if elevation did not improve model fit.

Species	**Size-growth relationship**	**$\Delta \mathrm{AIC}_c$ – size**	**$\Delta \mathrm{AIC}_c$ – elevation**
Abies amabilis	Monomolecular	2548.78	8.12
Tsuga heterophylla	Ricker	2391.35	0.32
Pseudotsuga menziesii	Ricker	294.68	0
Thuja plicata	Ricker	176.63	4.33

Figures

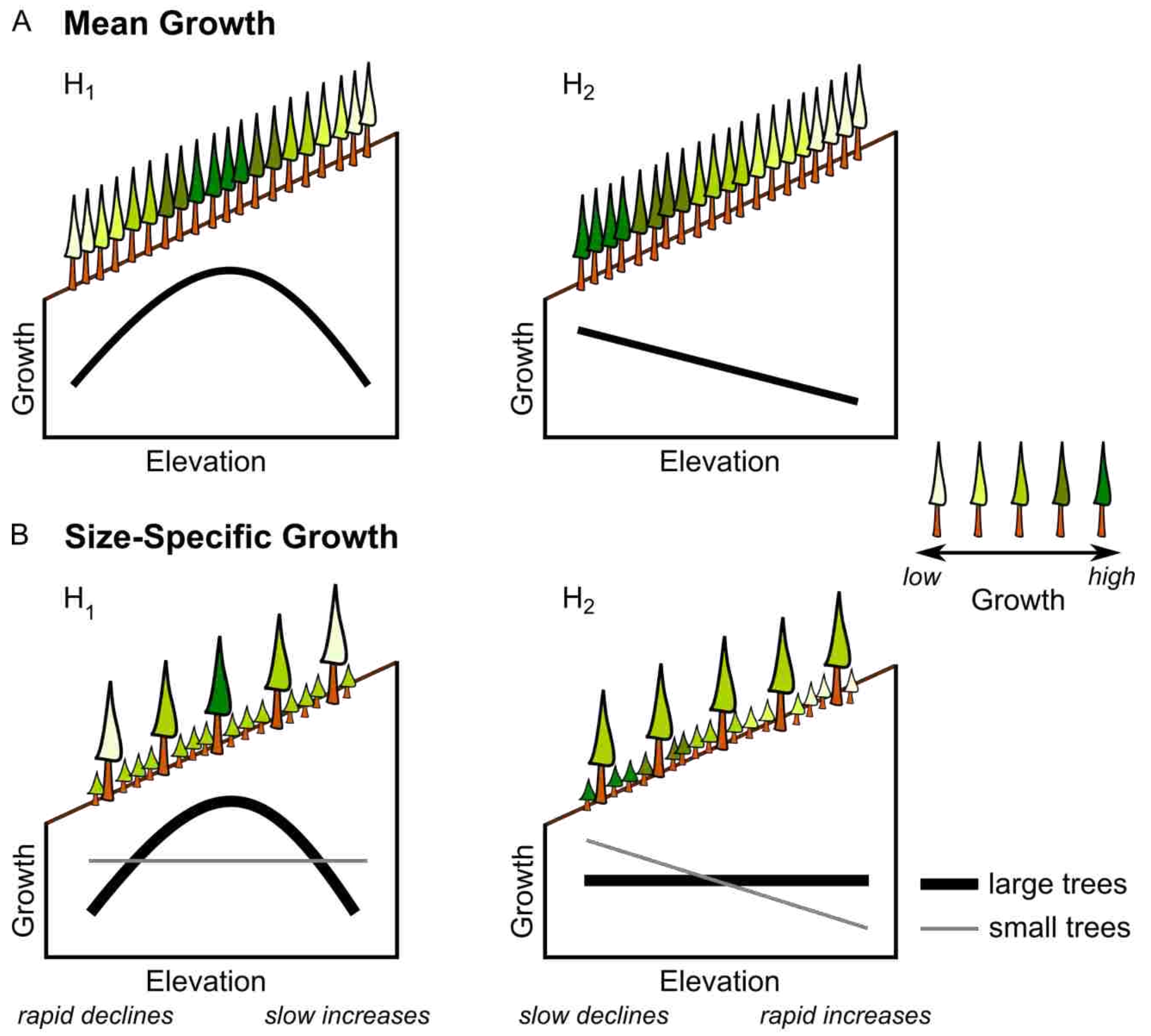

Figure 1. Potential growth patterns across a tree species elevational range. (A) Two hypotheses of how mean growth varies across elevation. H_1: growth is highest at the range core and depressed at the margins (as commonly assumed by ecologists). H_2: growth declines monotonically with increasing elevation due to increasing climatic stress. (B) Hypothetical examples of how size can mediate elevation-growth relationships, which can affect species responses to warming. H_1: large tree growth varies with elevation, but small tree growth does not. This pattern could result in rapid declines in population density at lower range margins with warming because adult growth is negatively related to temperature in this part of the range, and slow increases in population density at expanding upper margins because the growth of small/young individuals is insensitive to differences in climate. H_2: the growth of small trees declines with elevation, while large tree growth is constant. This pattern might lead to slow declines in population density at lower range margins because large tree growth is relatively insensitive to climate differences, and rapid increases in population density at high range margins because small/young individuals would likely grow rapidly in response to warming as low temperature stressors are relieved.

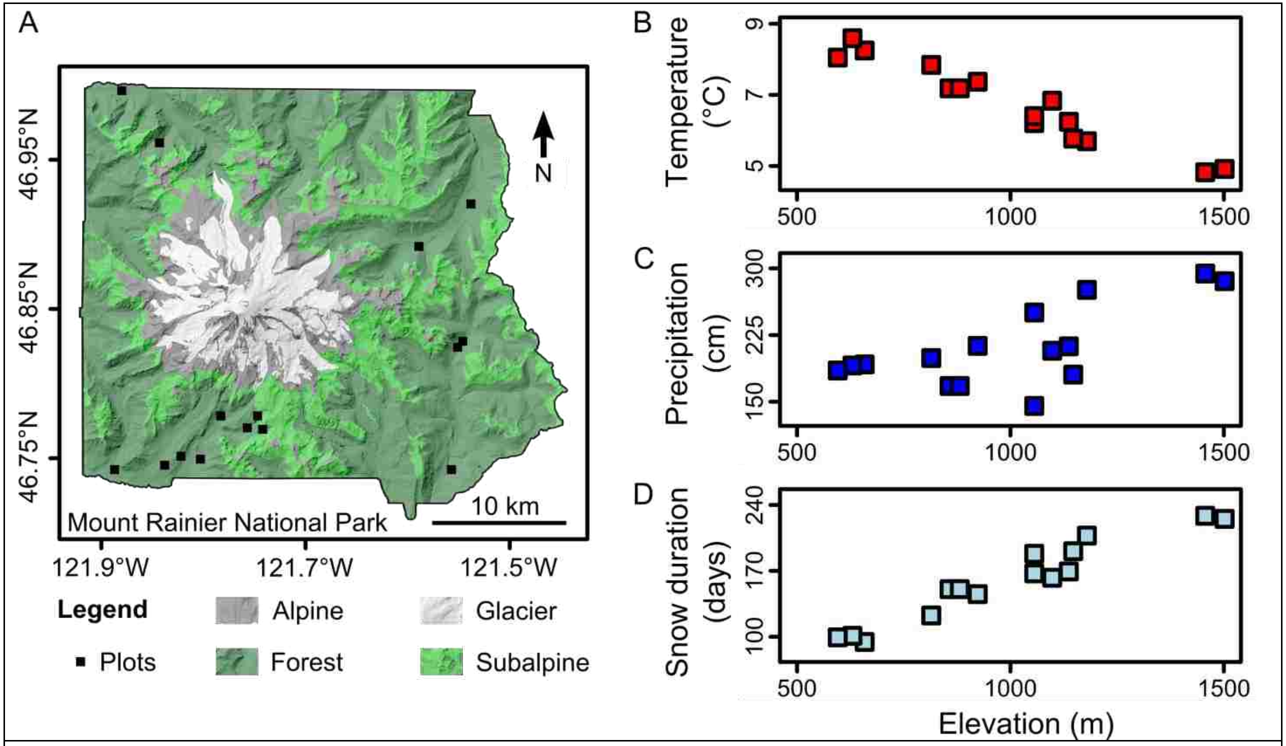

Figure 2. (A) Map of Mount Rainier National Park, showing study plots. The panels on the right show the climate of the plots across elevation: (B) mean annual temperature, (C) mean annual precipitation and (D) mean annual snow cover duration. See Appendix A for more details.

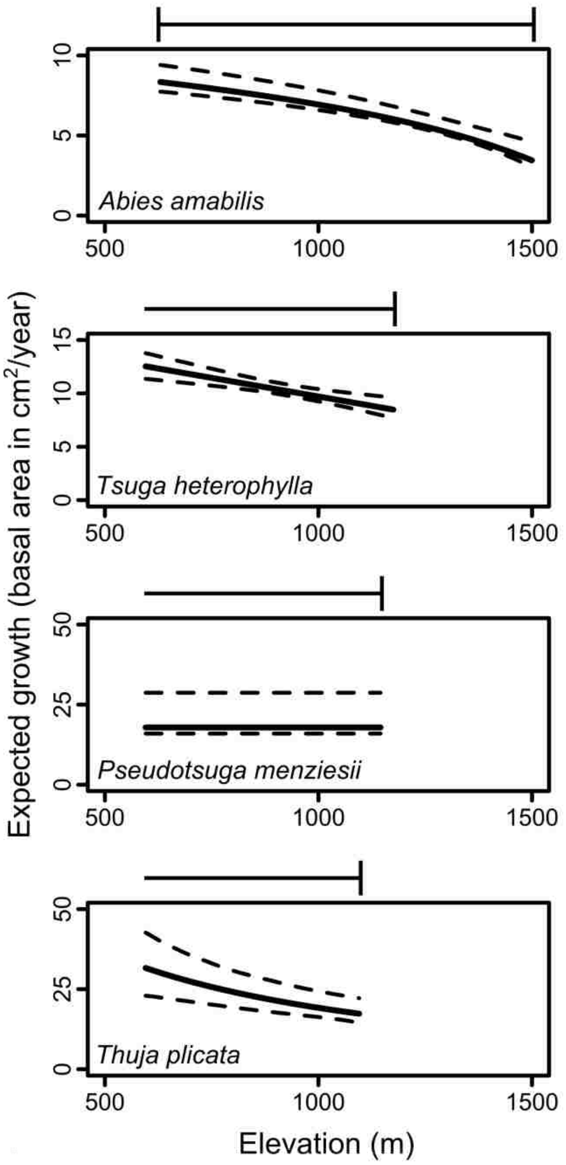

Figure 3. Relationship between elevation and growth for the four focal species. Solid lines show expected mean annual growth rates while dashed lines show the 95% bootstrap confidence interval. Bars above the graphs show the elevational range of the species within the study, with the "|" indicating that the range margin of the species in the study is near its range margin in the vicinity of Mount Rainier.

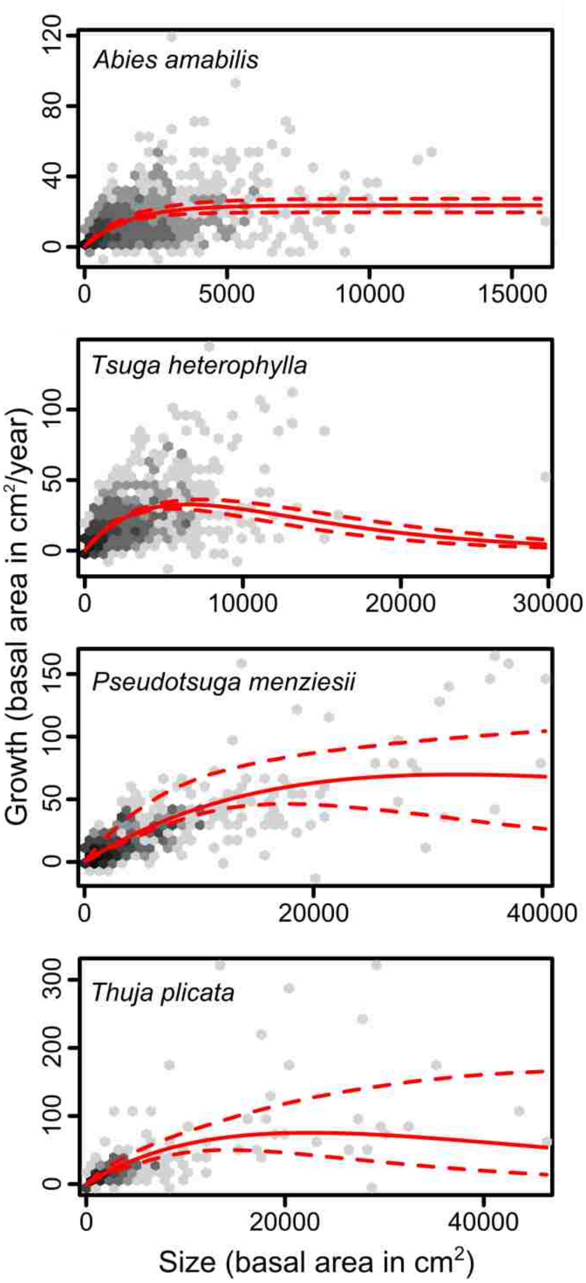

Figure 4. Relationship between individual size and growth. Hexagons show the density of data points, with darker shades indicating higher numbers of observations. Solid lines show expected annual growth rates while dashed lines show the 95% bootstrap confidence interval. For reference, 1,000 cm^2 basal area (BA) = 36 cm diameter at breast height (DBH); 5,000 cm^2 BA = 80 cm DBH; 10,000 cm^2 BA = 113 cm DBH; 20,000 cm^2 BA = 160 cm DBH; and 40,000 cm^2 BA = 226 cm DBH (Appendix E).

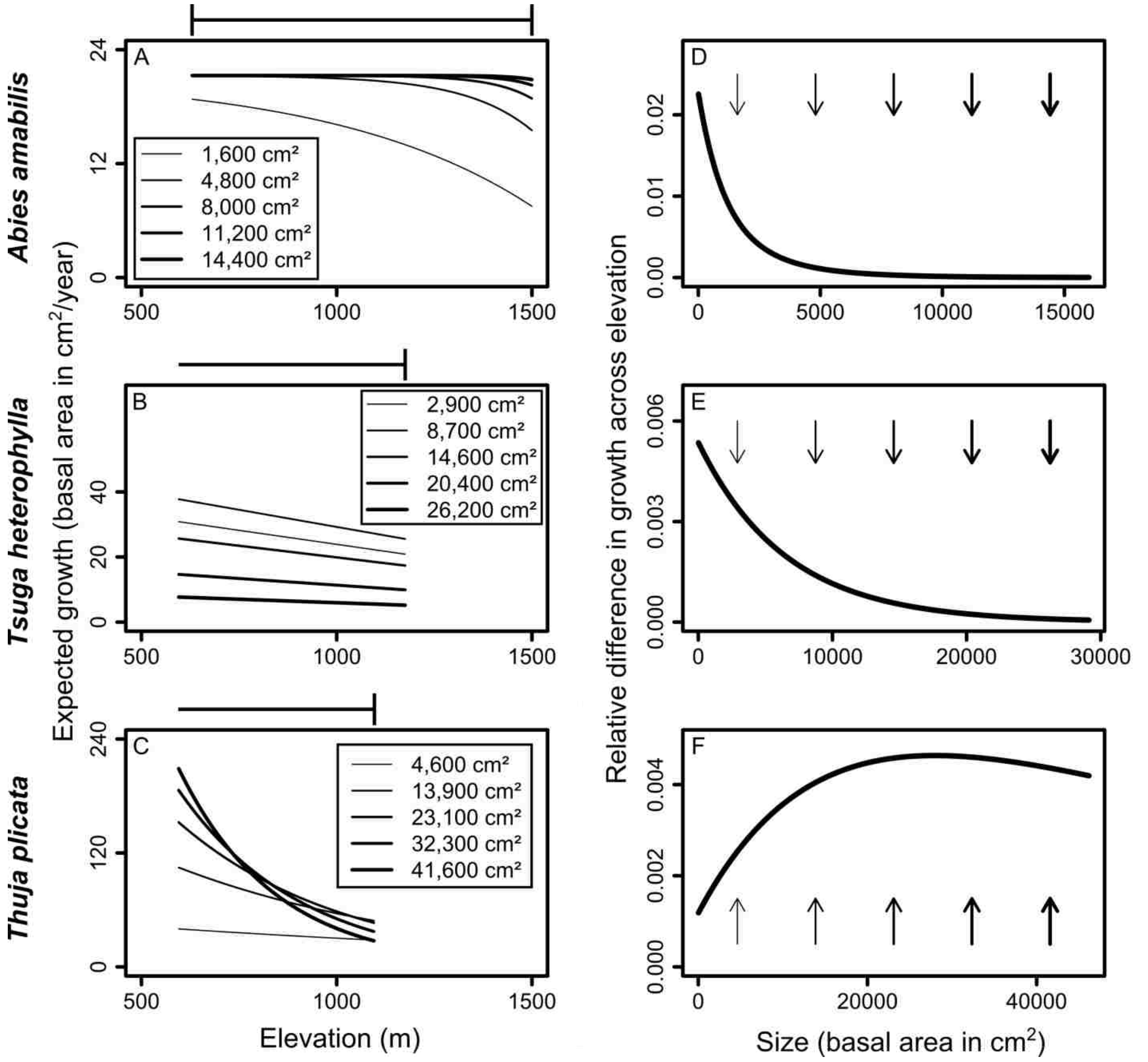

Figure 5. The relationship between size and elevation-growth relationships for the three species in which mean growth varied with elevation. The left panel (A-C) shows the elevation-growth relationship for trees from different size classes (curves are labeled according to basal area). Bars above the graphs show the elevational range of the species within the study, with the "|" indicating that the range margin of the species in the study is near its range margin in the vicinity of Mount Rainier. The right panel (D-F) shows differences in growth between trees at lowest versus highest plots the species were found in, relative to size. The locations of the arrows along the horizontal axes correspond to the midpoints of the size classes given in the legends in the left column. For reference, 1,000 cm^2 basal area (BA) = 36 cm diameter at breast height (DBH); 5,000 cm^2 BA = 80 cm DBH; 10,000 cm^2 BA = 113 cm DBH; 20,000 cm^2 BA = 160 cm DBH; and 40,000 cm^2 BA = 226 cm DBH (Appendix E).

Supporting information

Appendix A. Study plots used in this study

Table A1. Temperature and precipitation estimates were obtained using the PRISM climate mapping model (Daly et al. 2008) and daily records of temperature and precipitation at the Longmire climate station located within Mount Rainier National Park (http://lwf.ncdc.noaa.gov/oa/climate/climatedata.html). Snow duration was estimated using the SNOW-17 snow model (Anderson 1976). A more detailed description of the methods used to estimate these climate variables can be found in Ettinger et al. (2011). Relative abundance is in terms of number of individuals.

						Relative abundance			
Plot	**Elevation (m)**	**Mean annual temperature (°C)**	**Mean annual precipitation (cm)**	**Snow duration (days)**	**Stand age (years)**	*Abies amabilis*	*Tsuga heterophylla*	*Psuedotsuga menziesii*	*Thuja plicata*
TO11	595	8.1	185	92	550	0.0%	83.1%	7.7%	8.2%
TA01	630	8.6	191	93	250	3.0%	58.4%	34.6%	0.5%
TO04	658	8.3	192	87	750	17.0%	71.8%	2.0%	5.2%
TB13	815	7.8	199	115	150	3.4%	57.6%	27.9%	11.1%
AV02	857	7.2	168	146	1,000	84.7%	14.3%	0.3%	0.5%
AO03	881	7.2	168	146	1,000	72.3%	24.7%	0.7%	2.4%
AG05	923	7.4	213	139	650	40.4%	31.7%	3.1%	16.2%
AB08	1056	6.4	145	165	750	8.3%	67.5%	4.7%	17.9%
AV06	1056	6.2	250	186	750	63.2%	34.7%	0.8%	0.8%
AX15	1098	6.8	207	159	150	1.1%	58.3%	31.7%	8.8%
AV14	1137	6.2	212	167	1,200	53.2%	45.7%	0.0%	0.0%
PP17	1147	5.8	181	190	550	0.7%	11.3%	23.2%	0.0%
AM16	1179	5.7	276	206	600	57.0%	7.1%	0.0%	0.0%
AE10	1456	4.8	294	228	300	50.3%	0.0%	0.0%	0.0%
AR07	1502	4.9	286	225	330	36.3%	0.0%	0.0%	0.0%

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Appendix B. Size distributions of the focal tree species

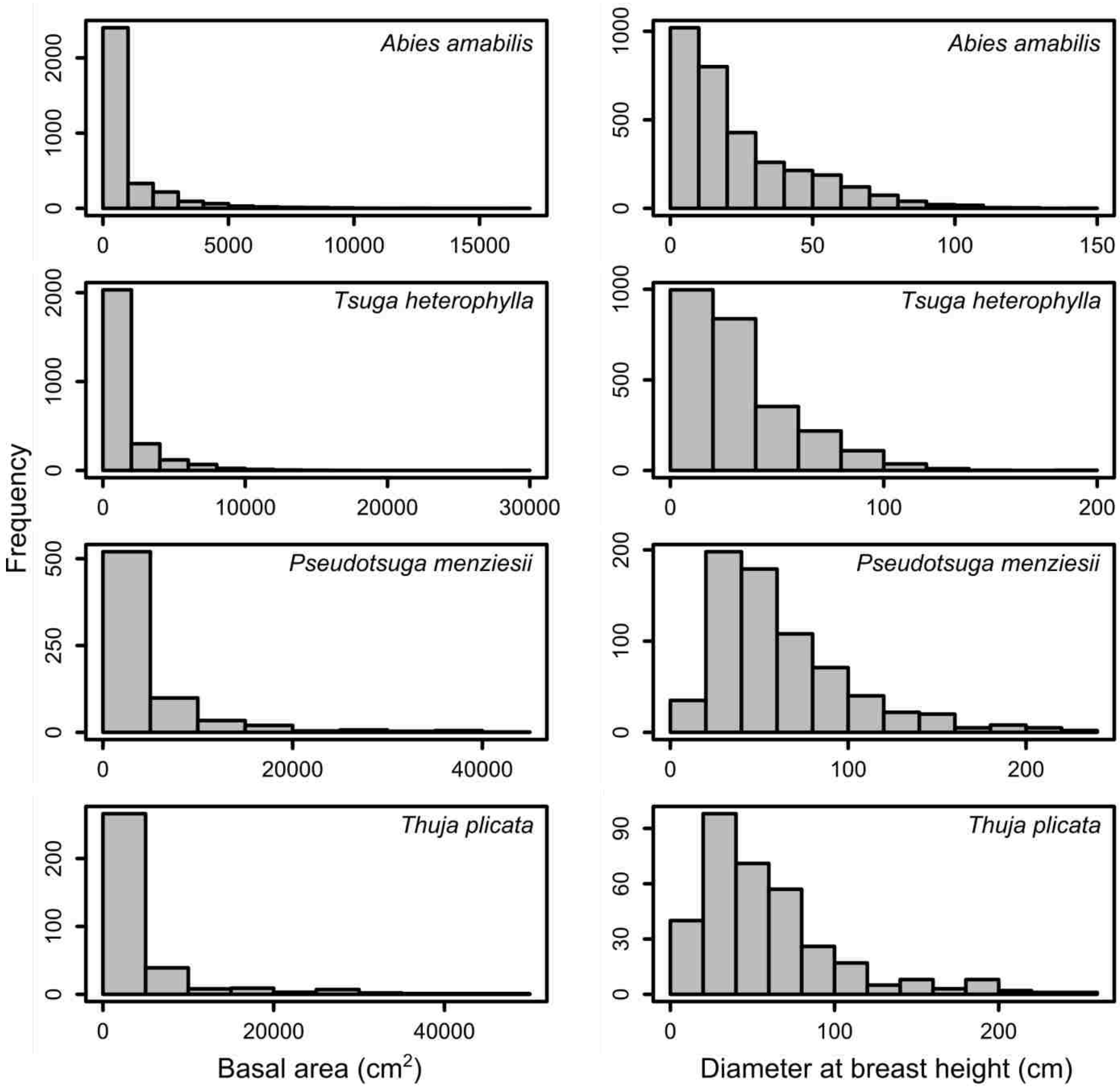

Figure B1. Size distributions of the four focal tree species in terms of basal area (left column) and diameter at breast height (right column).

Appendix C. Candidate models for the size-growth relationships

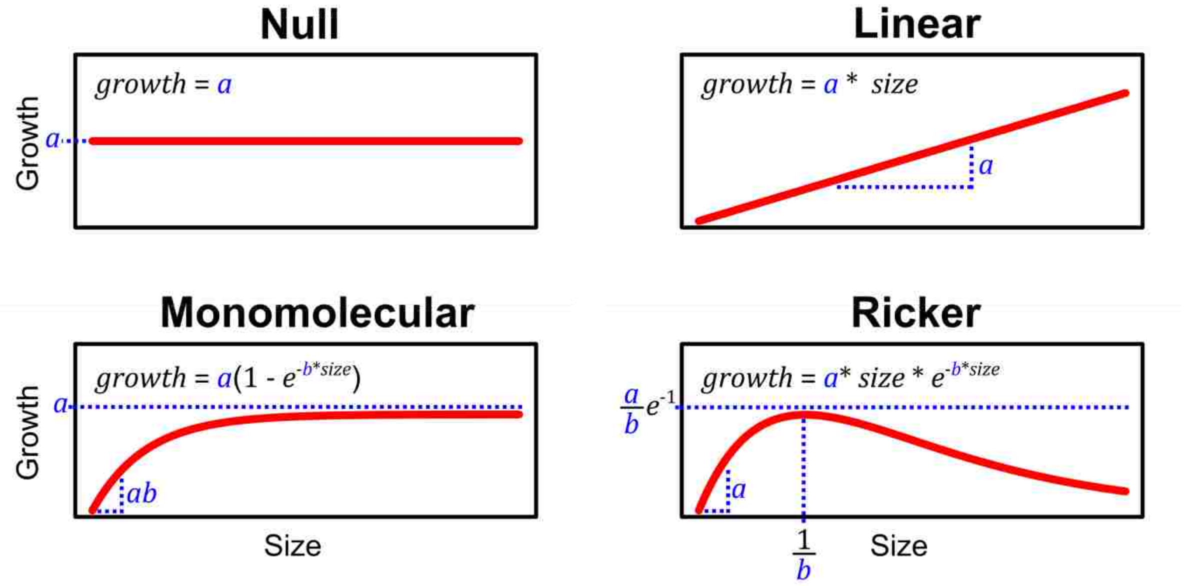

Figure C1. The four candidate models describing tree size-growth relationships. Size was calculated in terms of basal area while growth was calculated in terms of annual basal area increment. Note that the intercept was set at zero for all models except the null. Parameters (shown in blue) could themselves each be null, linear or quadratic functions of elevation.

Appendix D. Raw data for the relationships of growth and size with elevation

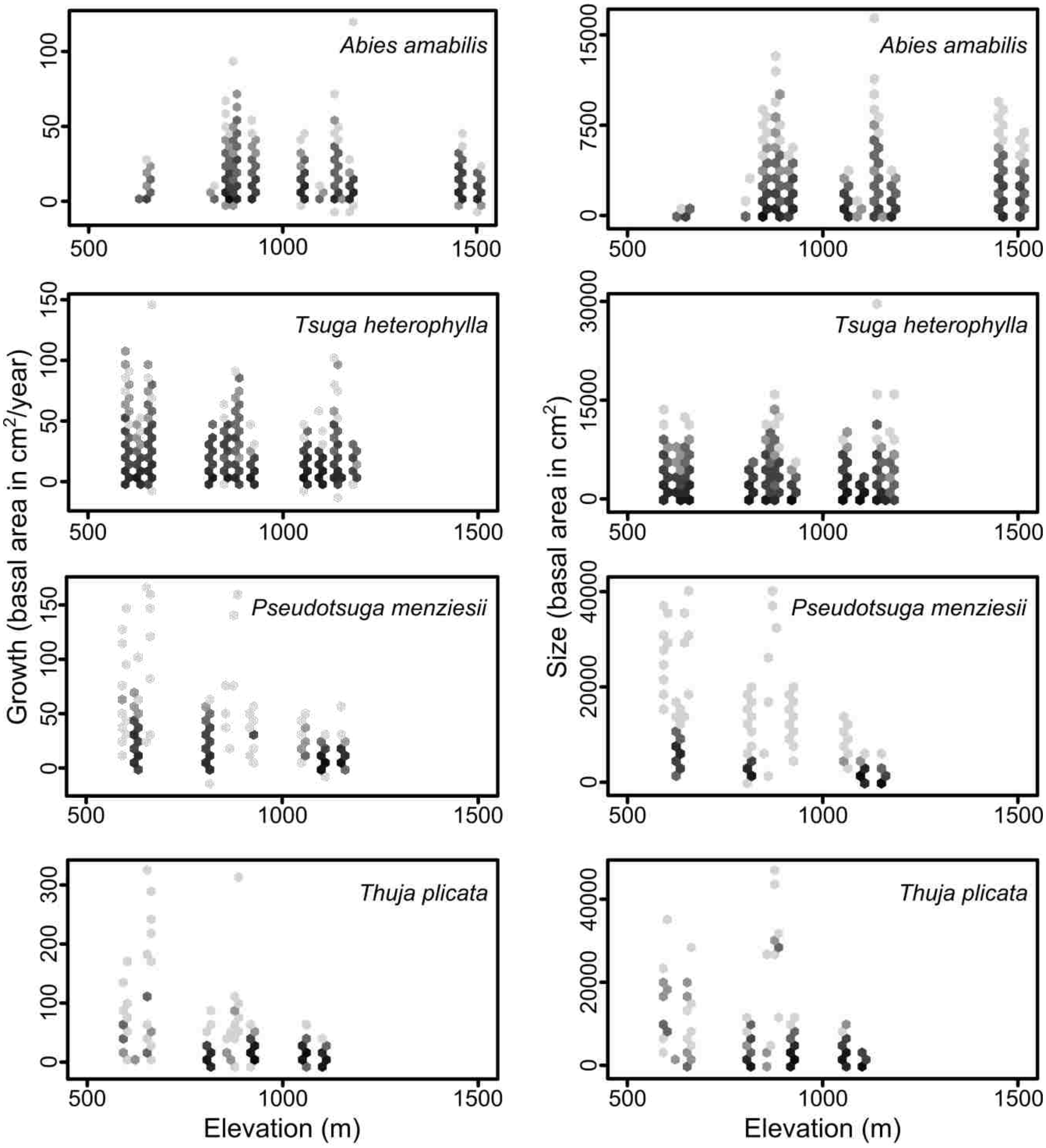

Figure D1. The raw data for the relationships between elevation and growth (left column) as well as elevation and size (right column) for the four focal species. The hexagons show the density of data points on the plot, with darker shades indicating higher counts of data points.

Appendix E. Relationship between basal area and diameter at breast height

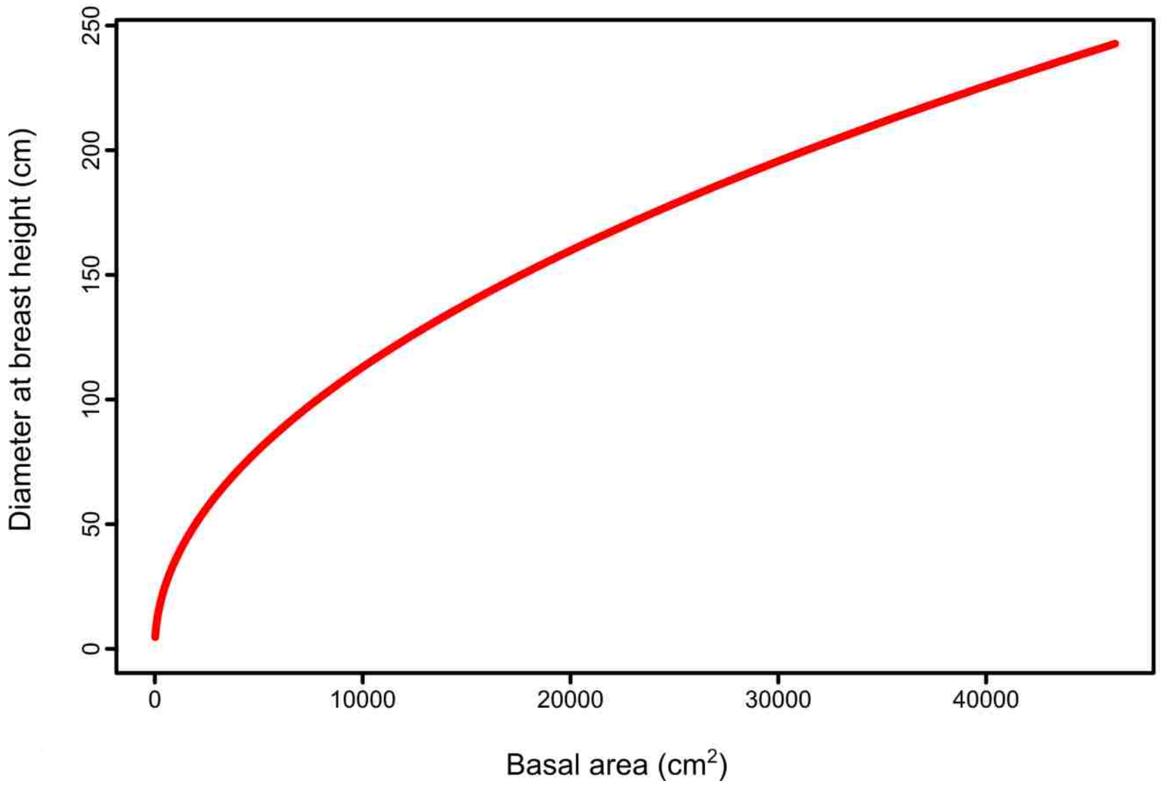

Figure E1. The relationship between basal area and diameter at breast height over the range of tree sizes observed in this study.

Appendix F. Size-growth relationships

Here we compare our approach to modeling size-growth relationships in trees to the approach of Stephenson et al. (2014). In our analyses, we expressed size as basal area and growth as the increase in basal area. On the other hand, Stephenson et al. (2014) expressed size as $\log_{10}$(mass) and growth as increase in mass. In our study, we showed that growth generally increased with size at a *decreasing* rate. Stephenson et al. (2014) showed that growth generally increased with size at an *increasing* rate. This difference in the shape of the size-growth curves between the two studies is due to differences in how size and growth are expressed, and not due to differences in the biological relationships. To demonstrate this, in Figure F1we present our data in terms of basal area for size and increase in basal area for growth in the left column (as it is shown in our main paper), and present the exact same data in terms of $\log_{10}$(mass) for size and mass increase for growth in the right column (as it is shown in Stephenson et al. – 2014). When our data are expressed in the way used by Stephenson et al. (2014), they also show a general pattern of growth increasing with size at an *increasing* rate. To estimate the mass of trees in our dataset, we used the diameter at breast height (DBH) measurements and taxon-specific allometric equations that relate total aboveground biomass to DBH (Jenkins et al. 2003).

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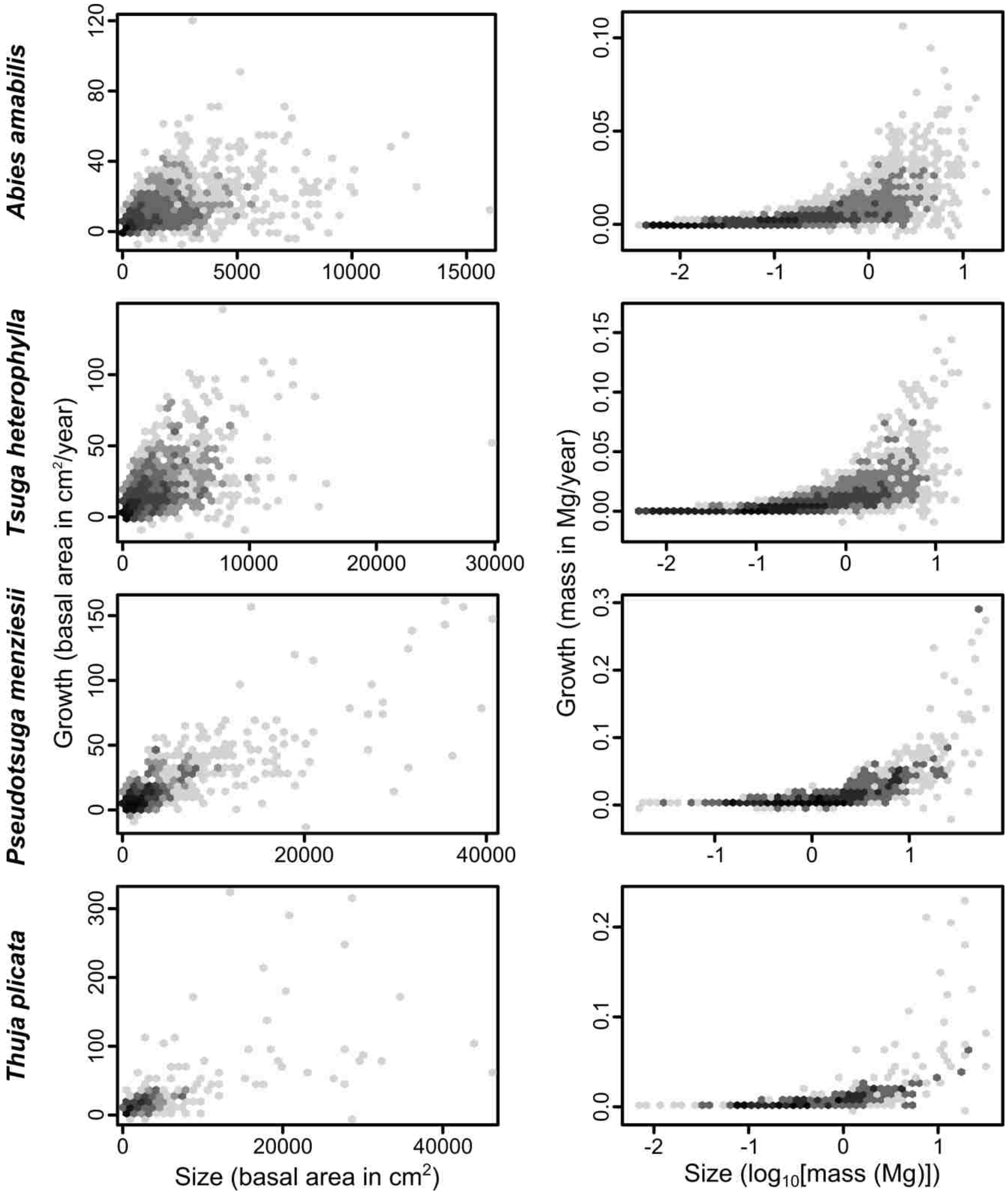

Figure F1. The size-growth relationship for trees at Mount Rainier. The left and right columns show the exact same data, but expressed with different measures of size and growth. In the left column, size is expressed as basal area and growth is expressed as increase in basal area (as it is in our main paper); growth generally increases with size at a *decreasing* rate. In the right column, size is expressed as $\log_{10}$(mass) and growth is expressed as mass increase (as it is in Stephenson et al. – 2014); growth generally increases with size at an *increasing* rate. Here, mass refers to the estimate of total aboveground biomass based on tree DBH and allometry.

Synthesis

Climate change at Mount Rainer National Park will result in complex changes in not only temperature and precipitation, but also the form of precipitation (snow versus rain), the timing of accumulation and loss of snowpack, and the nature and timing of extremes (both temperature or water related). My dissertation documents some of the features of these climate elements in the present-day and explores their potential impact on species establishment, survival and success. The impacts of climate change on the distribution and performance of plant species at Mount Rainier are likely to be large (Chapter 1), but are also likely to be complex due to the effects of other important factors such as topography and vegetation structure (Chapter 2), soil (Chapter 3) and life history (Chapter 4). Further research would help clarify some of these impacts.

In Chapter 2, we found that topographic heterogeneity in the subalpine and alpine biomes and structural heterogeneity of vegetation in the forest biome can lead to large differences in climate over small distances, which could buffer species from the impacts of climate change. These findings suggest that ongoing restoration and planting of native species at the Park might best be done across a variety of microhabitats to help ensure that some individuals are planted into locations that will remain suitable as climate change progresses.

But how might these two fine-scale drivers of climate (topography and vegetation) interact to affect microclimate patterns during periods of climate change? This interaction is likely to be particularly important in the subalpine parkland, where we have shown that topography has large impacts on climate and where vegetation structure is likely to change with climate change as trees establish in meadows. Thus, there is the potential for a complex interplay in which topography modifies the shifts in climate brought by warming, but warming also modifies vegetation structure, which would, in turn, modify climate differently according to topographic position. Measurements of microclimate variables in different combinations of topographic positions and vegetation structures would help elucidate these potential dynamics.

In Chapter 3, we found that the interaction of climate and soil had important effects on the establishment of young seedlings from subalpine and alpine species. Specifically, the results suggested that subalpine and alpine meadow species shifting up onto bare ground may be constrained by soil conditions, so that their ranges might contract at their lower limits (due to encroachment by trees) faster than they expand at their upper limits. Thus, the development of soil near the upper limit of the meadows could be critical for allowing meadow species to expand upward with climate change and maintain viable populations. At Mount Rainier, this soil development could be compromised by visitors hiking off maintained trails and forming “social trails” that both disturb the development of vegetation and accelerate erosion leading to soil loss. The results of this research therefore underscore the importance of the ongoing restoration and erosion prevention efforts conducted by the Park in the subalpine and alpine meadows. Our findings and the prospect of rapid climate change also suggest that managers might want to consider prioritizing restoration efforts near the upper limit of the meadows to better facilitate soil conservation and upward migration of meadow species.

But how do climate and soil affect the demographic rates of older individuals? Understanding the influence of climate and soil across the life cycle of these plants is important for predicting the long-term dynamics of these populations and biomes. This understanding could be gained by combining information on the seedling life stage from Chapter 3 with other information on older individuals. Sapling and adult growth rates could be inferred from tree rings, survival rates could be inferred from the growth rate measurements and observations of size structure in plant populations, and fecundity could be estimated from cone counts. The information from these different demographic rates across plant sizes could be combined using a structured population model (such as a matrix projection or integral projection model) to assess the influence of climate and soil on population dynamics. However, teasing apart the influences of climate and soil for older individuals would be difficult because it would not be possible to experimentally transplant individual plants to different combinations of climate and soil (as we did with the seedlings). Researchers would instead need to take advantage of natural variability in these two variables.

In Chapter 4, we found that individual size alters trends in tree growth across elevation, implying that different sized trees have different sensitivities to climate. Tree species also differed in their size-specific relationships with climate. In all, the results suggest that species are likely to shift their ranges individualistically in response to climate change, which could lead to the formation of novel forest communities with species assemblages that are not currently found in the Park or region. This prediction is consistent with observations from paleo-ecological studies which have found that novel forest communities can form during periods of climate change. Our results highlight the importance of conducting periodic and in-depth monitoring of the Park’s forests, because older surveys may become outdated and indicator species (such as the most abundant tree species in a location) may not have the same co-occurrence relationships with other species that they did in the past.

A more comprehensive picture of tree species population responses to climate change can be developed by incorporating the effects of climate on other vital rates, notably survival, fecundity and recruitment. These different vital rate models can then be combined to model overall population dynamics. This can be accomplished using integral projection models, as is being done with ongoing work in the Hille Ris Lambers lab, or with gap models that can also mechanistically incorporate the effects neighboring trees have on each through competition for resources such as light and soil moisture.

Perhaps the most daunting task for both the scientists conducting the research and the managers attempting to translate the research to practice will be convincing the public of the importance of this work, manifested through volunteering and funding, and altering their behaviors to support the natural and facilitated changes that will be occurring.