Implications of Climate Change for Turnover in Forest Composition

Author(s): Janneke HilleRisLambers, Leander D. L. Anderegg, Ian Breckheimer, Kathleen M. Burns, Ailene K. Ettinger, Jerry F. Franklin, James A. Freund, Kevin R. Ford and Steve J. Krolss

Source: Northwest Science, 89(3):201-218.

Published By: Northwest Scientific Association

DOI: http://dx.doi.org/10.3955/046.089.0304

URL: http://www.bioone.org/doi/full/10.3955/046.089.0304

Janneke HilleRisLambers[1], **Leander D. L. Anderegg**, **Ian Breckheimer**, **Kathleen M. Burns**, Biology Department, University of Washington, Box 351800, Seattle, Washington 98195

Ailene K. Ettinger, Department of Biology, Tufts University, 163 Packard Ave, Medford, MA 02155

Jerry F. Franklin, **James A. Freund**, School of Environmental and Forest Sciences, University of Washington, Box 352100, Seattle, Washington 98195

Kevin R. Ford, USDA Forest Service Pacific Northwest Research Station, 3625 93rd Ave SW, Olympia, Washington 98512

and

Steve J. Kroiss, Biology Department, University of Washington, Box 351800, Seattle, Washington 98195

Implications of Climate Change for Turnover in Forest Composition

Abstract

Predicting how climate change will influence forests is challenging. Forest communities are expected to lose cold-adapted trees near their low latitude/elevation range limits, while warm-adapted trees should increase in abundance near their high latitude/elevation limits (i.e., 'thermophilization'). However, slow-growing and long-lived trees, paired with climatic sensitivities that differ by species could add complexity to these predictions. To address these possibilities, we use demographic data collected from Mount Rainier National Park to examine: 1) the likelihood of rapid population growth or decline near range limits; 2) differences in climatic sensitivities between tree species at juvenile and adult stages; and 3) whether forest communities have already changed in response to recent warming. Our results suggest focal species are unlikely to shift their ranges rapidly with warming because recruit densities are low and time to reproductive maturity slow near upper range limits, while survival of adult trees is high near lower range limits. Additionally, focal tree species differ in the magnitude and strength of responses at seed and adult stages to climatic factors likely to be altered by warming. Consistent with these findings, shifts in forest community composition over the last 35 years were small, and not consistent with thermophilization predictions. In all, results imply that climate change will only have small, but unpredictable impacts on forest composition in the near-term. We discuss the possibility of much larger changes in forest composition with future climate change, if the drastically different climate regimes projected for the region fundamentally alter demographic processes and disturbance regimes.

Keywords: climate change, community assembly, demography, old-growth, Pacific Northwest

Introduction

How will climate change alter forest communities in the Pacific Northwest? The ubiquity of range shifts, both in response to contemporary warming (Rochefort and Peterson 1996, Harsch et al. 2009, Chen et al. 2011) and post-glacial warming (Dunwiddie 1986, McLachlan and Brubaker 1995, Gavin et al. 2001) imply that climate plays an important role in determining tree species range limits, and thus, local forest community composition. With dominant species in Pacific Northwest forests differing in climate sensitivities, warm-adapted and drought-tolerant tree species therefore seem likely to increase in Pacific Northwestern forest communities with climate change, at the expense of more cold-adapted and moisture-loving species. Forest communities may already be responding to warming, as temperatures have already increased by 0.7 °C since the 1900's (Dalton et al. 2013), causing snowpack to decline and water stress to increase in the region (Pederson et al. 2011).

How might we expect forest communities to have changed with recent warming, and to change with future climate change? We advance three possibilities. First, changes in Pacific Northwest

---

[1] Author to whom correspondence should be addressed.
Email: jhrl@uw.edu

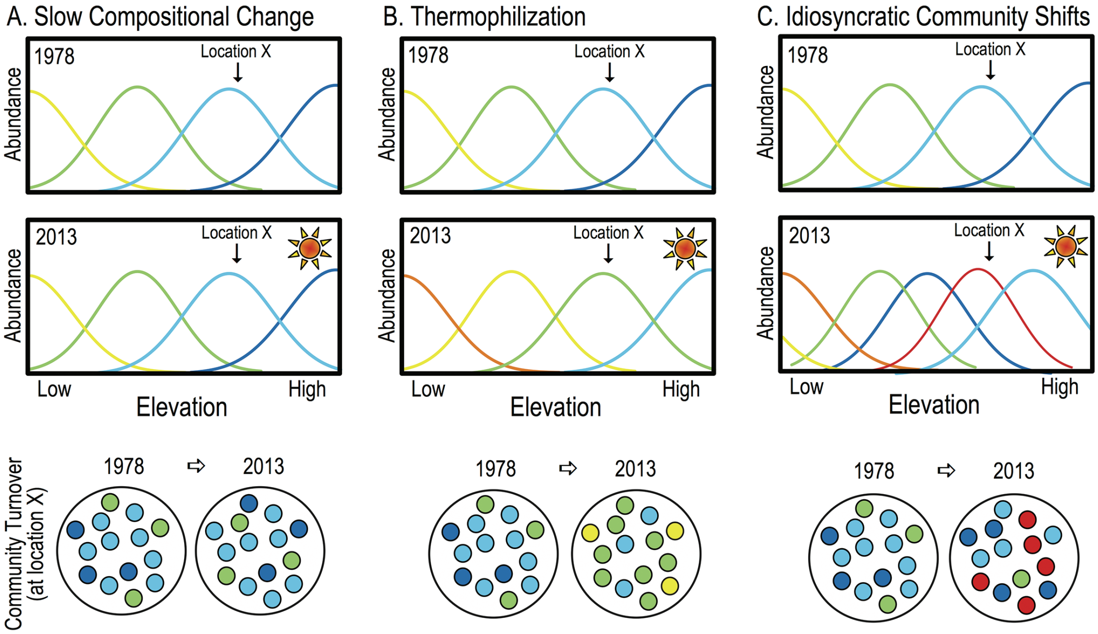


Figure 1. Climate change may have different effects on forest composition, depending on how the distributions of individual species shift in response to warming. For example, if range shifts of individual species are lagged with respect to warming due to slow rates of range expansion and contraction, forest community composition at a particular location may not change much with warming (lefthand panel). However, if range shifts of all species keep pace with warming, forest communities may experience thermophilization—an increasing abundance of warm-adapted tree species at the expense of cold-adapted species (middle panel). Finally, if range shift rates differ among species (due to differential lagged responses) or species have different climatic sensitivities (potentially implying different range shift directions), forest community changes may be idiosyncratic with respect to current climate-distribution relationships (righthand panel).

forest communities may be slow (Figure 1A), if long generation times and limited dispersal cause significant lags in range shifts relative to changes in climate (Gavin and Hu 2006, Svenning et al. 2008). Indeed, community change has been found to lag climate change in some cases (Bertrand et al. 2011, Gavin et al. 2013); consistent with the high proportion of species whose ranges have not shifted despite a half century of warming (Parmesan 2006). Alternatively, plant communities may become 'thermophilized', that is, increasingly dominated by warm-adapted and drought tolerant species (Figure 1B). This would occur if species ranges' readily and predictably shift uphill and poleward without significant lags. Recent studies in the Blue Mountains of Oregon have found such shifts in community composition (Damschen et al. 2010, Harrison et al. 2010). Finally, it is also possible that climate change will cause idiosyncratic shifts in forest community composition that are not predictable from current temperature-composition relationships (Figure 1C; Davis and Shaw 2001, Williams and Jackson 2007). This could occur if differences in species' sensitivity to changing climate, spatial differences in rates of climate change, or differences in migration capacity cause species ranges to shift individualistically (e.g., some species shift poleward/upward and some species shift equatorward/downward). Because each of these scenarios has different implications for our ability to generalize how forest communities in the Pacific Northwest will respond to warming, it is important to understand which is most likely.

In this study, we analyzed extensive demographic and compositional data collected across a large elevational gradient in the forests of Mount Rainier National Park (Figure 2). We addressed three objectives, which together allowed us to

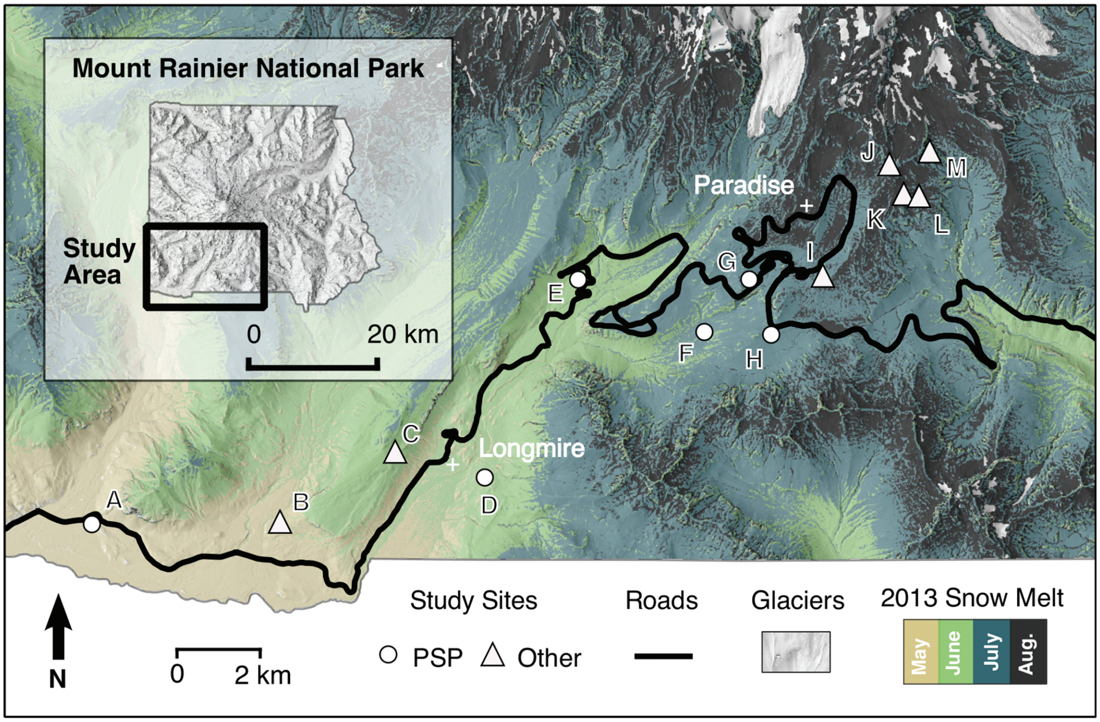


Figure 2. Study locations on the south side of Mount Rainier National Park, relative to snow melt date in 2013. Snowmelt date was estimated from a linear mixed-effects model which relates year, topography and vegetation cover to 4 years of data from a microclimate sensor network (~150 sensors). Circles represent the six 100 x 100 meter permanent stands in which forest composition was been censused seven times between 1978 and 2013. Triangles represent additional sampling locations where adult tree mortality, seed and germinant densities, and/or annual growth histories were collected, depending on the focal species (see methods and Appendix A for more details).

explore how moist temperate forest communities of the Pacific Northwest might respond to future climate change. Our first objective was to assess the likelihood of rapid population growth or decline at upper and lower range limits, necessary for range shifts, and thus, rapid changes in community composition. We did this by quantifying 1st year seedling densities (at upper range limits), time to reproductive maturity (at upper range limits), and adult tree survival (at lower range limits) for focal tree species. Although these are not the only vital rates that influence population growth rates, they represent demographic filters that influence range expansion and range contraction rates. Our second objective was to assess the possibility of idiosyncratic changes in forest communities in response to warming. We did this by asking whether tree species respond differently to climatic factors likely to be influenced by climate change, at either juvenile or adult stages, implying species-specific responses to warming. Our final objective was to determine whether forest composition in six old-growth forest stands has already responded to recent warming (over the last 35 years), and if so, whether changes are consistent with the 'thermophilization' of forest communities (i.e., Figure 1B).

Methods

Study Area and Focal Species

We quantified demographic rates, climatic sensitivity and compositional turnover for focal tree species occurring in moist temperate coniferous forests at Mount Rainier National Park. Forests in Mount Rainier National Park are characteristic of old-growth forests in the western Cascades, with the relatively low tree diversity, a dominance of conifers, and trees of large size (> 100 cm at diameter breast height) consistent with other forests in the region (Lutz et al. 2013). Fire initiates most stand development, but tends to be infrequent although often high in severity (Hemstrom and Franklin 1982). At smaller spatial scales and shorter time scales, canopy gaps created by the mortality of one or a few individual trees influence regeneration, but large gaps are relatively rare (Larson and Franklin 2010). We assume forests at Mount Rainier National Park have experienced approximately 0.7 °C warming in the last century, consistent with the rest of the Pacific Northwest (Dalton et al. 2013).

Mount Rainier is an ideal location for this study, because its elevation (4.3 km in height) guarantees forests that cover large climatic gradients (Figure 2). Additionally, Mount Rainier has been a National Park since 1899, and its forests have remained relatively free from direct human disturbance. Long-term data on forest composition (collected since the late 1970s) and spatially extensive data on forest compositional turnover across climatic gradients are available (Franklin et al. 1988, Acker et al. 2006, Larson and Franklin 2010), allowing us to assess whether compositional turnover over time in recent decades is consistent with compositional turnover along spatial climatic gradients.

To address objectives 1 and 2 (population dynamics at range limits, sensitivity to climatic factors), we focused on six conifer species: Pacific silver fir (*Abies amabilis*), Alaska cedar (*Callitropsis nootkatensis*), Douglas fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and mountain hemlock (*Tsuga mertensiana*). We assessed climatic sensitivity at adult stages for one additional species, Subalpine fir (*Abies lasiocarpa*), which is the dominant species in the treeline ecotone at Mount Rainier National Park. Collectively, these focal species dominate forests throughout the moist coniferous forest biome in the Pacific Northwest and make up > 80% of basal area in most stands within Mount Rainier National Park (Franklin et al. 1988). For objective 3, we considered all tree species with individuals > 15 cm dbh (10) occurring in six mature or old-growth permanent stands. The seven tree species we focused on for objectives 1 and 2 are collectively the most abundant species in these six stands.

Study Locations

All demographic measurements took place along the south slope of Mount Rainier (Figure 2), along a > 1000 meter elevational gradient. With increasing elevation, temperatures and growing degree days decline, while precipitation, snowpack size and snow duration increase (Figure 2). Most measurements were taken in permanent forest stands (100 x 100 meter stands) established in old-growth forests between 1976 and 1978, as part of the Pacific Northwest Forest Permanent Sample Plot Network (Acker et al. 2006, Larson and Franklin 2010), with recruitment and adult climate-growth relationships additionally quantified at several other locations (Figure 2, Appendix A) (See supplementary appendices at the end of this article [online only].)

Measurements and Statistics

Objective 1: Demographic Rates—For recruitment, we assessed germinant densities for focal tree species annually from 2009–2013, in six permanently marked 1 m^2 plots spaced 5 m apart along a linear transect in the center of 100 x 100 meter forest stands. Germinants were identified to species by their cotyledons at peak germination, between 3–4 weeks after snowmelt. We surveyed germinant densities in nine forest stands in total (see objective 2), but restricted our analyses for this objective to those stands in the upper third of each species range (as determined from a previous forest survey—Franklin et al. 1988, see also Appendix A). An important caveat is that our estimates of recruitment at range limits for high elevation species (*Abies amabilis, Callitropsis nootkatensis, Tsuga mertensiana*) is based on six seedling plots surveyed over five years (30 m^2 surveyed in total), and is therefore limited by sampling effort (estimates for lower elevation species were based on 18 seedling plots surveyed over five years—90 m^2 surveyed in total). We then used linear mixed-effects models, assuming germinants were distributed as a zero-inflated negative binomial distribution (with log link) with year and plot random effects (Zuur et al. 2009, Kroiss and HilleRisLambers 2015). This allowed us to estimate germinant densities (per m^2) and differences among species in germinant densities at and above upper elevational range limits (defined by the presence of adult trees). Models were fit using the glmer function in the lme4 package in R (R Core Team 2015).

To attain a minimum estimate of the time it takes to reach reproductive maturity at upper range limits, we also collected cross sections of 20 100–150 cm tall individuals (saplings) at upper range limits of three species: *Abies amabilis*, *Tsuga heterophylla,* and *Tsuga mertensiana* (Appendix A, Ettinger and HilleRisLambers 2013). Saplings were located at least 20 meters apart from each other. Cross sections were sanded, scanned, and ages quantified using the program WinDENDRO (version 2008e, Regent Instruments, Quebec City, Quebec, Canada). We then calculated average annual height growth increments by dividing height at the time of harvest by estimated minimum age obtained from counting annual rings, and used this value to estimate each individual's age at 200 cm. We consider the time it takes for a sapling to reach 200 cm to be a lower bound on the time to reproductive maturity, as most focal tree species at Mount Rainier do not produce cones until they are taller than this. We also used this estimate because we did not wish to extrapolate more than 33% beyond the maximum sized individuals we harvested (~150 cm). We then fit a linear model with a response variable of age and species as explanatory variable to assess whether species differed in time to reproductive maturity (Bolker 2008).

To estimate survival rates at lower range limits within Mount Rainier, we modeled annual survival for six of the focal species using data from the lowest elevation permanent stand in which the species occurred and there were an adequate number of individuals (> 20 individuals—Figure 2, Appendix A and B). These stands are close to the true lower elevational range limits for three species (*Abies amabilis, Callitropsis nootkatensis, Tsuga mertensiana*), but not for the three species whose ranges extend to elevations below the lowest elevation of the park (*Pseudotsuga menziesii, Thuja plicata, Tsuga heterophylla*). We fit a generalized linear model of average annual survival with species identity as the explanatory variable, using a binomial error distribution with a logit link function to calculate the mean survival rate of each species and the 95% confidence intervals (Bolker 2008). These models were fit using the glmer function in the lme4 package in R. To assess the significance of pairwise differences in survival amongst species, we performed multiple comparison tests using the multcomp package (Hothorn et al. 2008).

Objective 2: Climatic sensitivities—To assess how microclimate influences germination rates, we quantified seed density in a 0.176 m^2 seed trap adjacent to each of the six 1 m^2 plots (per stand) in which we estimated germinant densities from 2009–2013 (six seed trap-seedling plot pairs in each of nine total forest stands—Figure 2, Appendix A). Seed trap contents were collected in early spring prior to seedling germination, and represent seeds available for germination since dispersal occurs throughout fall and winter and focal species do not possess a persistent seedbank (Burns and Honkala 1990, Bonner and Karrfalt 2008).

We also quantified snowpack duration and soil moisture at each plot, two annually varying climatic factors likely to influence germination. Both variables likely covary with other abiotic or biotic variables that also influence germination. Snow duration (number of days that snow covered the ground, per year) was determined with HOBO temperature loggers placed on the soil surface (measuring temperature every 3 hours). Since snow acts as an insulator, temperatures of 0 °C that are diurnally constant indicate sensors are covered by snow (Ford et al. 2013, Raleigh et al. 2013). Soil moisture was measured using a Decagon Devices ECH$_2$O Check soil moisture probe (5 cm in length). Missing values of soil moisture and snowpack duration were estimated from models fit to an extensive microclimate dataset on Mount Rainier including data from these nine stands as well as nine others (r^2 between predicted and observed is 0.81 for soil moisture and 0.99 for snow duration—Kroiss and HilleRisLambers 2015). Soil moisture and snow duration coefficients for each species were qualitatively similar when we repeated analyses excluding observations with missing microclimatic variables.

We used these data to investigate how seed germination (probability of germination) is influenced by snow duration and soil moisture with one analysis per species, using a linear mixed-effects model with a binomial error distribution and logit link, and seed trap location and year as random effects (Zuur et al. 2009, presented in Kroiss and HilleRisLambers 2015). We estimated the number of seeds available for germination in each plot (i.e., the size in a binomial trial) from seed counts in adjacent traps in the previous year (as focal species do not possess a persistent seed bank), scaled to 1 m^2 and rounded to the nearest whole number. We examined the effects of our microclimate variables (snowpack and soil moisture) on germination across species' entire elevation ranges (i.e., across all 9 stands) to take advantage of both spatial and temporal variation in explanatory variables. We only fit these models for seed trap/plot combinations with seeds in seed traps or germinants in plots (observations of zero germinants and zero seeds is not accommodated by a binomial distribution). When germinant densities were nonzero and greater than estimated seed inputs (problematic for binomial distributions), we set the number of seeds available for germination to the number of germinants found (thus assuming 100% germination). We verified that results were qualitatively similar when we excluded these observations (10% of the total data set). All microclimatic predictors were standardized and centered prior to analysis for the ease of interpretation. These models were fit using the glmer function (lme4 package) in R (R Core Team 2015).

To determine climatic sensitivities of focal adult trees, we collected increment cores from 20 trees per focal species adjacent to the stands closest to the upper range limits for three species whose upper range limits occur within closed canopy forests (*Pseudotsuga menziesii, Thuja plicata, Tsuga heterophylla*—Appendix A and B), and visited one higher elevation site to collect 20 cores per species for the three species with range limits close to treeline (*Abies amabilis, Callitropsis nootkanensis, Tsuga mertensiana*—Appendix A and B). These data were presented in two previous studies (Ettinger et al. 2011, Ettinger and HilleRisLambers 2013). For *Abies lasiocarpa*, whose upper range limit extends to tree line and beyond the elevational range of the monitoring plots, we collected 20 cores from four sites near tree line (Figure 2). Two cores per individual were sanded, and then scanned with a high-resolution scanner using the program WinDENDRO (Version 2008e; WinDENDRO 2008) to measure annual growth rings to 0.001 mm (Regent Instruments, Quebec City, Quebec, Canada). Cores were visually and then statistically crossdated using the dplR package (Bunn 2010) in R (R Core Team 2015). We averaged ring widths from the two collected cores for each individual tree, then standardized each tree's ring width series by fitting a spline through the time series to remove size-specific trends (100 year rigidity, wavelength cutoff 50%—Cook and Peters 1981). We assessed the adult growth sensitivity of each species to annual climate variables by combining detrended unitless ring width indices data with climate data. Climate data came from either the Longmire Ranger Station (for all species but *A. lasiocarpa,* years 1914–2007) or Paradise Ranger Station (for *A. lasiocarpa,* years 1918–2010), corrected to each site using the 30 year climate normal of the gridded PRISM dataset (Parameter-elevation Regressions on Independent Slopes Model—Daly et al. 2008).

We used linear mixed-effects models (one analysis per focal species) to assess the relationship between annual ring width indices (RWI) of each individual and various growing season (May–Sept.) and dormant season (Nov.–March) precipitation and temperature related variables (Zuur et al. 2009, see Ettinger et al. 2011 for a full description of models tested). We designated both individual tree and year as random effects to account for non-independence of data from the same individual or within years, and fit standardized climate variables as fixed effects. We used mixed-effects models instead of more standard dendroecological analyses (where climate sensitivities are extracted from average RWI's across all individual cores within a stand) because we wanted to account for tree-to-tree variation in their responses to climate. We applied AIC-based model selection of candidate mixed-effects models, which revealed that focal species were sensitive to dormant season snowpack related variables and growing season temperature variables, with annual maximum Snow Water Equivalent (SWE) and Growing Degree Days (degree days > 5 °C, GDD) the most effective predictor variables (these variables were included in the best fit model for 6 of 7 species and 4 of 7 species, respectively). Thus, we fit a model with SWE and GDD as explanatory variables separately for each species, calculating the 95% confidence intervals model coefficients using the lme4 (Bates and DebRoy 2004) and lmerTest packages in R (R Core Team 2015).

Objective 3: Compositional Turnover Over the Last 35 Years—To determine how forest communities at Mount Rainier may have already changed in response to recent warming, we examined compositional turnover in six permanent forest stands (circles in Figure 2), established in old-growth forests along the south slope of Mount Rainier as part of a larger long-term monitoring effort (Acker et al. 2006, Larson and Franklin 2010). In 1978, all individual trees > 15 cm in these 100 x 100 meter stands were identified to species with sizes measured. Six recensuses have been conducted since then (1983, 1988, 1993, 1998, 2007/2008, 2012/2013), with mortality events, growth of surviving trees, and recruitment of new individuals into the > 15 cm dbh size classes measured. We used these data to estimate basal area (in cm^2 m^{-2}) of all > 15 cm dbh trees in each stand in each of the censuses (i.e., over 35 years).

Our goal was to determine whether compositional turnover observed in these stands is consistent with recent climate change in the Pacific Northwest (Dalton et al. 2013). We used an extensive data set of forest community composition (463 plots) collected between 1976 and 1980, approximately the same time frame that permanent forest stands were established (Franklin et al. 1988), to generate an expectation for compositional turnover with warming for each of the six permanent stands. Plots differed slightly from permanent stands—for example, they were circular (rather than square) and smaller than the permanent stands (ranging from 375 to 1000 m^2), and individual trees under 120 cm dbh were binned by size rather than having exact diameters measured. See Franklin et al (1988) for more details on sampling.

To determine how forest composition (i.e., relative abundance of tree species as a proportion of basal area) varied across climate gradients in the late 1970s, we used canonical correspondence analyses. We considered community composition of each plot to be the proportion of total basal area taken up by each of 16 tree species (see Appendix C for a list of species found). To generate climatic explanatory variables, we used the locations of each of the 463 plots to extract and downscale climate averages from a spatial climate model (PRISM—Daly et al. 2008). In brief, we estimated climate variables from a regression between elevation and PRISM values in the closest 25 PRISM grid points (every 800 meters), and used the elevation of each plot to estimate plot-specific climate values. We estimated several climatic variables for each plot, including mean and seasonal temperatures, mean and seasonal precipitation, snow duration and snow pack, and growing degree days. However, many of these climate variables were highly correlated (Appendix D), so we restricted our explanatory climatic variables to Mean Annual Temperature (MAT), Summer precipitation (Sumppt), and Winter precipitation (Wintppt). These climatic variables reflect potentially distinct constraints on tree growth (e.g., growing season length, summer moisture stress, winter damage) and are highly correlated with other climatic variables that may also control the distributions of some species (e.g., growing degree days, snowpack). We assessed the significance of the overall canonical correspondence analysis, individual ordination axes as well as the climatic explanatory variables using ANOVA-like permutation tests (Ter Braak 1986, Legendre and Legendre 2012).

Next, we used the species and environmental ordination scores from the canonical correspondence analysis of these 463 plots to 1) place forest community composition in 1978 and 2013 in each of the six permanent sample stands in environmental space and 2) predict the direction (and magnitude) of change in ordination space these stands should have experienced between 1978 and 2013 (the most recent census) assuming ~ 0.535 °C warming in the last 35 years (estimated based on observed warming rates between 1978-2011 in the region—Dalton et al. 2013). Warming in this time period is not uniform, but significant and well within the range of annual climate variability experienced historically (Dalton et al. 2013). This allowed us to assess whether temporal shifts in forest community composition in the last 35 years are consistent, both in direction and magnitude, with compositional turnover across spatial gradients in climate in 1978. These analyses and were conducted using the cca, anova.cca and predict.cca functions in the vegan package in R (R Core Team 2015).

Results

Objective 1: Demographic Rates

Germinant densities at upper elevational range limits were extremely low for all species, but there was considerable variation among species (Table 1). For three of the focal species (*Thuja plicata, Pseudotsuga menzesii, Callitropsis nootkatensis*), we never located a single germinant at or above their upper elevational range limit, despite seeds being present in adjacent seed traps for two of those species (*Pseudotsuga menziesii, Callitropsis nootkatensis*). For the other three species (*Abies amabilis, Tsuga heterophylla*, *Tsuga mertensiana*), germinant densities varied among species by as much as two orders of magnitude. The majority of these germinants are likely to die before their second year (results not shown).

We found that time to reproductive maturity at upper range limits (i.e., minimum age at 200 cm in height) differed among species (ANOVA: $F_{\text{species}} = 5.291$, $P = 0.008$, Table 1), but was generally quite long (consistent with estimates from Antos et al. 2000). *Abies amabilis* averaged 124 years to reproductive maturity, which was significantly longer than both *T. mertensiana* (89 years, $P = 0.024$, based on Tukey multiple comparisons of means test) and *T. heterophylla* (86 years, $P = 0.014$) at their upper range limits. Time to reproductive maturity did not differ

TABLE 1. Species-specific demographic processes that could slow climate change-induced range shifts include recruitment rates and time to reproductive maturity at upper range limits, and survival at lower range limits. Values are shown with 95% confidence intervals in parentheses. Low germinant densities (column 2) at upper range limits imply recruitment limitation could slow range expansions into climatically suitable habitats. Range expansions may be additionally constrained by slow rates of reproductive maturation at upper range limits (column 3). Finally, high survival rates at the lower range limits (column 4) may slow range contractions. Note, in three cases germinants were never recorded at upper range limits (column 2), resulting in infinite 95% confidence intervals.

Species	Germinant density (per m^2, at upper range limit)[1]	Age at 2 m height (in years, at upper range limit)[2]	Survival rates (annual, at lower range limit)[3]
Thuja plicata	0 (0, Inf)	NA	0.993 (0.988, 0.996)
Pseudotsuga menziesii	0 (0, Inf)	NA	0.996 (0.994, 0.998)
Tsuga heterophylla	0.072 (0.018, 0.283)	86 (66, 105)	0.984 (0.981, 0.987)
Abies amabilis[4]	3.40 (0.874, 13.223)	124 (105, 144)	0.983 (0.975, 0.989)
Callitropsis nootkatensis[4]	0 (0, Inf)	NA	0.997 (0.994, 0.998)
Tsuga mertensiana[4]	0.326 (0.066, 1.6184)	89 (69, 108)	0.995 (0.990, 0.997)

[1] From censuses of first year seedlings

[2] From ring counts of saplings

[3] From individuals in tagged and recensused in permanent forest stands (100 x 100 m) between 1978 and 2013.

[4] Based on 5 years of seedling censuses conducted in 6 1 m^2 seedling plots in one forest stand. We do not believe this limited sampling effort influences our conclusion that recruitment is low at upper range limits, as seedling densities for these species are low throughout our study site (2.37, 1.45, and 2.58 seedlings per m^2, respectively).

between *T. mertensiana* and *T. heterophylla* (*P* = 0.97). These estimates are much greater than those reported in the silvicultural literature for *T. heterophylla* and *A. amabilis* (20–30 years: Burns and Honkala 1990), which is likely explained by the slower growth of individuals that occur at higher elevations and in more competitive environments than managed stands.

All focal species had high mean annual survival rates, with narrow 95% confidence intervals in the stands near their lower elevation limit (Table 1). Mean survival rates varied from 0.9827 (*Abies amabilis*) to 0.9965 (*Callitropsis nootkatensis*). The lowest lower 95% confidence interval was 0.9747 (*Abies amabilis*) while the highest upper 95% confidence interval was 0.9979 (*Pseudotsuga menziesii* and *Callitropsis nootkatensis*). The survival rates of *Pseudotsuga menziesii*, *Callitropsis nootkatensis,* and *Tsuga mertensiana* were significantly higher than those of *Tsuga heterophylla* and *Abies amabilis*, though there were no significant differences within those two groups ($\alpha = 0.05$, Table 1). The survival rate of *Thuja plicata* did not differ from any other species ($\alpha = 0.05$, Table 1).

Objective 2: Climatic Sensitivities

Snowpack duration and soil moisture both affected germination rates, but the significance and direction of the relationship varied among species (Figure 3). For example, snowpack duration positively affected germination for one species (*Thuja plicata*) but negatively affected germination for two species (*Tsuga heterophylla* and *Tsuga mertensiana*). Overall, effects of snowpack duration on germination were larger than the effects of soil moisture (Figure 3). Both snowpack duration and soil moisture are likely to be correlated with other abiotic and biotic variables that could influence germination (e.g.,

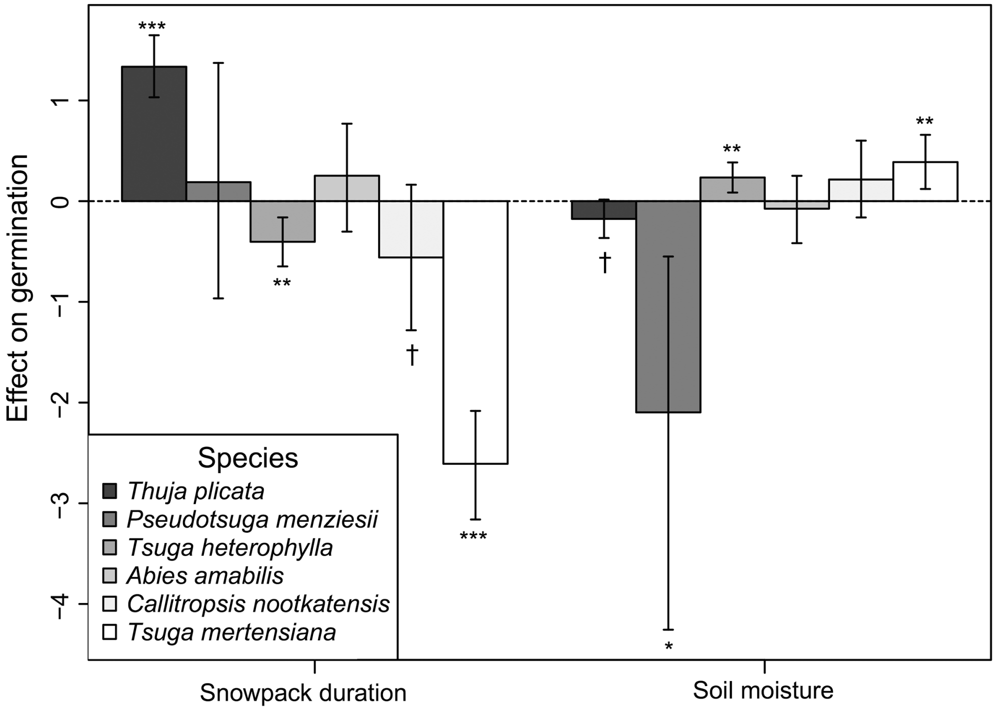


Figure 3. Effects of abiotic microclimate variables (snowpack duration and soil moisture) on germination rates. All variables were standardized prior to analysis, making the height of different bars directly comparable. Error bars represent 95% confidence intervals. Significance from the full models (including all explanatory variables) are indicated with asterisks and/or crosses, which denote significance levels († = $P < 0.10$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$). Species are ordered from left to right by increasing elevation of their range centers. Data represent a subset of that published in Kroiss and HilleRisLambers (2015).

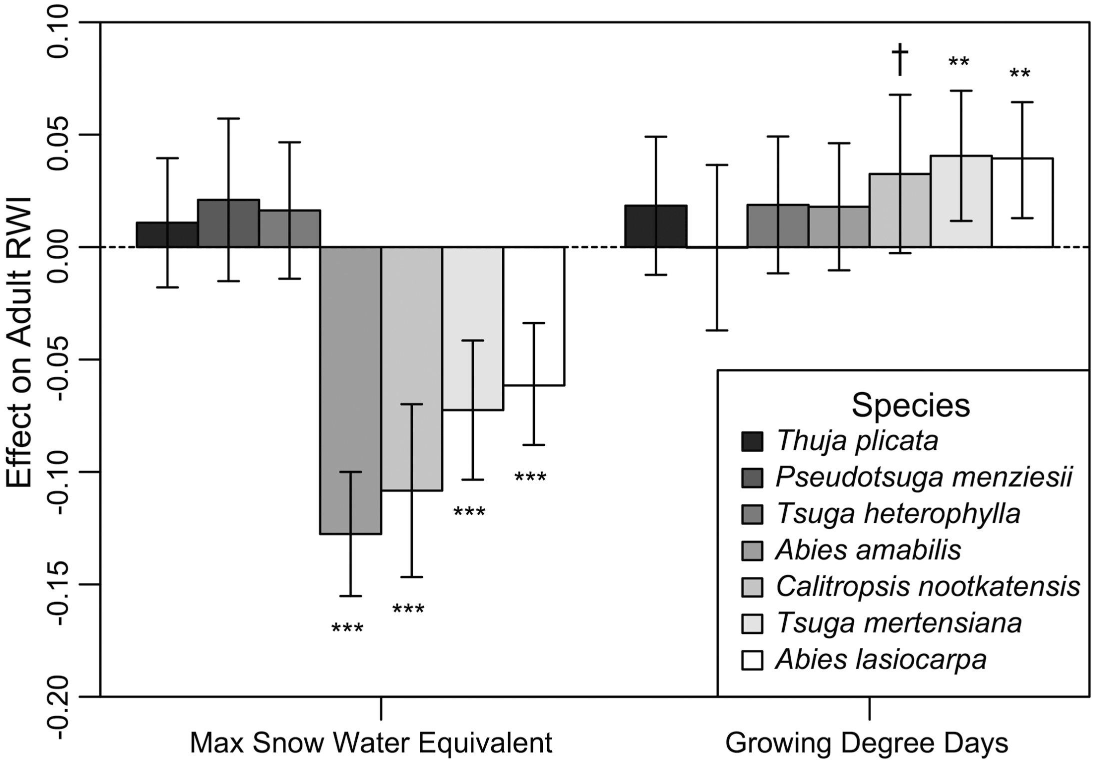


Figure 4. Effects of maximum snow water equivalent and annual growing degree days on annual adult tree growth (detrended ring width index, RWI). All variables were standardized prior to analysis, making the height of different bars directly comparable. Error bars depict the 95% confidence intervals for parameter estimates, and asterixes and/or crosses denote significance levels († = $P < 0.10$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$). Species are ordered from left to right by increasing elevation of their range centers. Data for all species but *Abies lasiocarpa* also published in Ettinger et al. (2011) and Ettinger and HilleRisLambers (2013).

light, fungal pathogens, Appendix D), thus, the causal nature of these relationships must be interpreted with caution.

Warm growing-season temperatures (as measured by growing degree days) consistently had positive effects on tree growth, whereas a large snowpack (as measured by high snow water equivalent) had consistently negative effects on tree growth (Figure 4). However, the strength of effects differed among species, with high elevation trees (those whose upper range limits are at or close to treeline) strongly affected by one or both climatic variables, and low elevation trees (those whose upper range limits are within closed canopy forests) weakly or unaffected by both climatic variables (Figure 4). Overall, snowpack had larger effects on growth than did growing degree days, presumably reflecting the extraordinarily large amounts of snow received on the south slopes of Mount Rainier. Because climatic variables covary (Appendix D), the mechanistic drivers of variation in tree growth may be different climatic variables than the two we examined.

Objective 3: Compositional Turnover Over the Last 35 Years

Canonical correspondence analyses indicate that forest community composition varies across the large environmental gradients found at Mount Rainier National Park (Figure 5A), with ordination axis 1 generally corresponding to gradients in mean annual temperature and winter precipitation (which were correlated—Appendix D) and ordination axis 2 generally corresponding to a summer precipitation axis. The overall model was significant ($P < 0.005$), as were the first

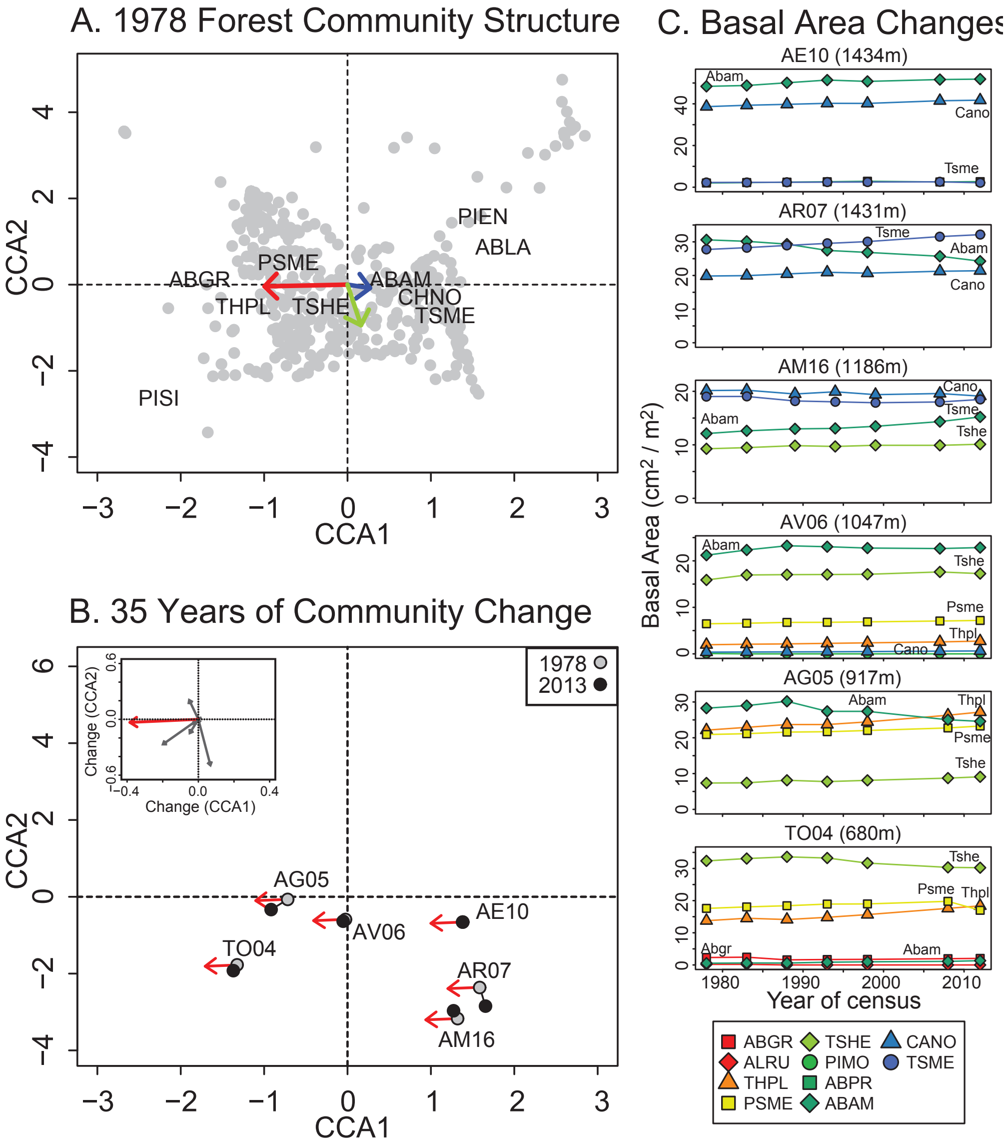


Figure 5. Forest composition at Mount Rainier National Park relative to climatic gradients (A), 35 years of compositional change for six old-growth forest stands along those same environmental ordination axes (B), and basal area change of component species in those same six old-growth stands (arranged from highest elevation on top to lowest elevation on bottom) during seven censuses between 1978–2013 (C). In A, light grey points represent species composition (proportion basal area) relative to climatic gradients in 463 375, 500 or 1000 m^2 circular plots censused between 1978 and 1980 (estimated using canonical correspondence analyses). Arrows indicate climatic gradients (red = MAT, mean annual temperature, dark blue = wintppt, winter precipitation, light green = sumppt, summer precipitation) and four letter codes place representative tree species relative to those climatic gradients (see Appendix C for species names). The same analysis was used to estimate the relative position of permanent stands (as predicted by species composition) in environmental space in 1978 (grey circles) and 2013 (black circles); as well as project the direction of expected shifts in ordination space with 0.535 °C warming (red arrows). In C, points and lines represent species-specific basal area in each census year, with symbol colors representing the contribution of each focal species—as identified in the legend (4 letter species codes explained in Appendix C). Colors for species in 5C are scaled by the position of species along ordination axis 1 (representing mean annual temperature—see 5A), with reds and yellows indicating species towards the warmer end of the ordination axis and greens and blues indicating species positioned towards the cooler end of the ordination axis.

two ordination axes (P = 0.005) and all three climatic factors (MAT P = 0.005, Wintppt P = 0.02, and Sumppt P = 0.005 respectively), as determined from pseudo-F values generated by permutation tests. The proportion of variance in tree species composition explained by the three climatic variables was small (i.e., constrained inertia score/total inertia: 10.07%), as is common for community ecological data sets. However, this value likely underestimates the true amount of compositional variation associated with ordination axes (Okland 1999).

Species positions on these ordination axes are consistent with broader biogeographic patterns (Figure 5A). For example, *Tsuga mertensiana* and *Abies lasiocarpa* (TSME and ABLA), located on the right (cold) side of ordination space, are the dominant treeline species at Mount Rainier National Park and occur into Alaska on the west coast (Burns and Honkala 1990). Similarly, *Picea sitchensis* (PISI), located on the bottom left (warm, wet) side of ordination space, is dominant in coastal temperate rainforests in the Pacific Northwest, while *Picea engelmannii* (PIEN) located on the top right (cold dry) part of ordination space, primarily occurs in high elevation dry forests east of the Cascade Crest (Burns and Honkala 1990).

Shifts in environmental ordination space associated with observed changes in forest composition were much smaller than the changes predicted by the 0.535 °C change (observed across the Pacific Northwest) in mean annual temperature (red arrows in Figure 5B—see also inset graph) for all but one stand (AG05). Moreover, composition in most stands did not shift in the direction predicted by (spatial) compositional turnover along environmental gradients in the late 1970's. This lack of change in ordination space is consistent with the low amount of compositional turnover (in terms of basal area) in the six permanent stands over the course of 35 years (Figure 5C). However, this lack of stand-scale change in basal area composition exists despite substantial turnover of individual trees in the forest stands, with 13.8–39.7% of the basal area in each stand in 2013 reflecting new basal area since 1978 (Appendix E), and between 10.4 and 36.2 % of basal area in 1978 lost by 2013 due to mortality of individual trees. Most of the new basal area accrued in that time was due to growth, not ingrowth (Appendix E). Turnover also varied amongst species and stands (Appendix E).

Discussion

Although forest community composition varies across the climatic gradients existing within Mount Rainier National Park, recent climate change has resulted in surprisingly little compositional turnover. This is largely consistent with observed low rates of recruitment and long generation times at upper range limits (implying slow range expansion rates), and high survival rates at lower range limits (implying slow range contraction rates). What compositional change has occurred is not consistent with current climate-composition relationships, potentially due to the differences we observed among species in their sensitivity to climatic factors at juvenile and adult stages. Although our results imply these forest communities have been resistant to recent climate change, we believe that compositional change may be much greater in the future, especially if rapid rates of climate change substantially increase compositional turnover through their direct impacts on demographic rates or indirect impacts on disturbance regimes. Below, we discuss these points in more detail.

Low Recruitment, Slow Maturation, and Mortality Imply Lagged Responses to Climate Change

Current demographic rates (Table 1) provide a possible explanation for why forest communities at Mount Rainier did not change much in composition over the last 35 years (Figure 5B and 5C), despite regional warming (Dalton et al. 2013). Compositional turnover requires the invasion of new species into areas rendered suitable by climate change, a change in relative abundance of existing species (through differential growth), and/or the local extinction of existing species in areas made unsuitable by climate change. Our results suggest that the range expansions and contractions leading to such invasions and extinctions are currently slow for focal tree species at Mount Rainier National

Park. First, there is limited recruitment at upper range limits (Table 1 and column 2). Of course, even low seedling densities will eventually lead to population establishment, but established individuals are also very slow to reach reproductive maturity (Column 3 of Table 1; see also Parish and Antos 2005), which is critical to moving invasion fronts forwards. Second, at current survival rates (Column 4 of Table 1; Larson and Franklin 2010, Acker et al. 2015), focal species can persist for a long time as adult trees at lower range limits, even if populations are declining. For example, at a survival rate of 0.983 (the lowest of our focal species), populations have a half-life of 40 years (i.e., 40 years for half of the individuals in a population to die).

If current demographic rates are maintained, our results therefore suggest that compositional change will continue to be slow. However, we did not study all demographic transitions of trees, some of which may have larger impacts on population growth rates in the future. Additionally, it is possible that the greater rates of climate change projected for the future will alter population dynamics such that range expansions and contractions will occur at faster rates in the future. For example, warming may increase germination and seedling survival, and is likely to increase sapling growth rates (Figure 3; Ettinger et al. 2011, Ettinger and HilleRisLambers 2013), hastening reproductive maturity and (potentially) increasing range expansion rates. Warming could also increase the possibility of episodic recruitment at or above range limits from individual trees that recruited during past climates (e.g., 'climate relicts'—Hampe and Jump 2011). Similarly, mortality rates may increase in Western US forests due to climate change (van Mantgem et al. 2009), which could decrease population growth rates at lower range limits, leading to range contractions. Thus, although our results are consistent with populations of our focal trees being slow to respond to future climate change, demographic data from all life history stages of trees, as well as an understanding of how those demographic rates will respond to climate change, will be required to fully understand the impacts of climate change on future population dynamics at range limits (e.g., Doak and Morris 2010, Merow et al. 2014).

Species-Specific Climate Sensitivities Imply Individualistic Responses to Climate Change

When changes to forest composition eventually occur, as is likely with continued climate change, our results suggest that compositional turnover in forests at Mount Rainier may not be predictable from current climate-composition relationships (e.g., Figure 5A). This is because focal tree species differ, both as juveniles and adults, in their likely demographic responses to the environmental factors that will are and will continue to be altered by climate change. For example, results suggest that declining snow will both positively and negatively affect germination of focal tree species (Figure 3, *Tsuga mertensiana* vs. *Thuja plicata*), implying that the range expansions (as influenced by seedling recruitment) could differ among tree species (consistent with Fisichelli et al. 2014). Declining snow and increasing growing degree days will likely lead to increases in growth of high elevation tree species (e.g., *Tsuga mertensiana*), but the effects of short-term warming on the growth of lower elevation species (e.g., *Tsuga heterophylla*) are likely to be weaker and less certain (Figure 4). These results imply that both range expansions (influenced by growth through influences on generation times) and range contractions (through links between growth and mortality—Wyckoff and Clark 2002) could vary among focal species, leading to compositional turnover that could be difficult to predict. These results are consistent with many other studies suggesting that species will respond individualistically to climate change in terms of range shifts, potentially leading to novel communities (Figure 1, Davis and Shaw 2001, Williams and Jackson 2007, Brusca et al. 2013).

There are many factors that we did not study that will also influence the likelihood of idiosyncratic community shifts (Figure 1C). For example, germination and tree growth may not strongly influence population growth rates; if so, whether or not species differ in climate sensitivity in the demographic rates that do (e.g., tree mortality, seedling survival) will ultimately determine whether community shifts are predictable from climate-composition relationships (Figure 5A). Similarly, differences among species in dispersal rates, which influence range expansion rates, could also influence community reassembly. Our focal species also differ in their shade tolerance and therefore regeneration dynamics under open vs. closed canopies (Burns and Honkala 1990). Although extremely large gaps are currently rare in these old growth forests (similar to Parish and Antos 2004), they may become more common in the future (Stewart 1986). If so, successional dynamics in larger gaps could dominate responses to climate change. Demographic models that incorporate climatic sensitivities at all life history stages (e.g., Doak and Morris 2010), dispersal, as well as the spatial consequences of successional dynamics may be needed to fully understand the extent to which climate change will result in community reassembly in old growth forests of the Pacific Northwest.

Little Compositional Turnover over the Past 35 Years

Despite significant warming in the Pacific Northwest in the last four decades (Dalton et al. 2013) and evidence that forest composition varies across climatic gradients (Figure 5A), the overstory composition of six forest stands in Mount Rainier National Park has not changed much (Figure 1, Figure 5B). Clearly, forest composition varies across the large temperature (and to some degree precipitation) gradients experienced by forests in Mount Rainier National Park. Moreover, the placement of species on ordination axes generated from Mount Rainier forest plots are largely consistently with the continental distributions of these species (e.g., *Abies grandis* vs. *Abies lasiocarpa*; *Picea sitchensis* vs. *Picea engelmannii*— Figure 5A), lending support to these climate-composition relationships. Warming would therefore be predicted to shift forest communities (compositionally) to the left in ordination space—towards warmer mean annual temperatures. However, despite significant growth and mortality in the six permanent stands (Appendix E), both the direction and magnitude of change (with one exception—AG05) in forest stands was not consistent with expected climate change driven compositional turnover (Figure 5B and 5C, see also Lutz et al. 2014).

Why did species composition in the six old-growth stands not change in the direction predicted by spatial turnover along a similar temperature gradient, despite recent regional warming (Dalton et al. 2013)? Many factors may have played a role. First, the amount of climate change experienced by trees in Mount Rainier National Park may be less severe than regional trends, particularly for seedlings in the forest understory that are often buffered from extreme temperatures (De Frenne et al. 2013, von Arx et al. 2013). Warming within Mount Rainier National Park may also have been less than the regional average (Appendix F), although trends from individual stations are often confounded by site and instrumentation changes. It is also possible that compositional change lags behind climate change, due to demographic inertia—that is, the limited ability of warm-adapted species to expand their ranges upward (despite newly suitable habit) and the persistence of cold-adapted species, despite warming (Svenning and Skov 2007, Bertrand et al. 2011). If so, 35 years may simply not be long enough in these forests for significant mortality of existing trees to provide opportunities for sufficient ingrowth into the 15 cm diameter class (through gap dynamics), thereby altering forest composition. Limited ingrowth in these stands paired with observed low recruitment and slow sapling growth of focal species are consistent with this hypothesis (Table 1, Appendix E). The species-specific and life history stage specific differences in climatic sensitivities we observed (Fig 3. Fig 4, Bell et al. 2014) may additionally have resulted in compositional turnover in a different direction than expected (e.g., AR07, AM16—Figure 5B). It is also likely that a combination of these factors are at play.

How Will Future Climate Change Influence Compositional Turnover?

How will forest communities at Mount Rainier National Park change in the future, given rapid rates of warming? Slow compositional turnover in the last 35 years suggests recent climate change has thus far not had strong impacts on forest community composition (at least for overstory trees > 15 cm dbh—Figure 5B, 5C). Moreover, demographic analyses suggest that population growth and decline of these species may not proceed rapidly in the future (Table 1), although a full demographic analysis of all life history stages would be needed to fully assess this possibility (e.g., Doak and Morris 2010, Merow et al. 2014). It might be tempting to conclude that these results imply old-growth forests in the wet Pacific Northwest (west of the Cascades) will be resilient to future climate change. We believe that it would be a mistake to come to such a conclusion, given that the magnitude of future climate change is projected to be 5–7 times greater than that observed in the last century (Dalton et al. 2013). Such large changes in climate could potentially speed up population dynamics of focal conifers, and thus, compositional turnover. For example, although adult tree mortality rates of focal species are currently low (Table 1), mortality may increase with climate change (van Mantgem et al. 2009), opening up the forest canopy and increasing recruitment and growth rates of understory trees.

The indirect effects of future climate change on forest communities could have additional and even larger impacts for compositional turnover. In particular, warming could influence fire frequencies and pest or pathogen outbreaks at Mount Rainier National Park, as they have in other parts of the Western United States (McKenzie et al. 2004, Kurz et al. 2008, Littell et al. 2010, Devine et al. 2012). Fire and forest pathogens (both insects and fungal diseases) could eliminate adult trees, thereby providing opportunities for new species to recruit and become established (Stewart 1986, Cwynar 1987, Franklin et al. 1991, Stueve et al. 2009, Weed et al. 2013, van Mantgem et al. 2013, Gavin et al. 2013). Successional dynamics following such disturbance could hasten the replacement of cold-adapted and drought-sensitive species by warm-adapted and drought-tolerant species. When and whether compositional change at Mount Rainier National Park will accelerate in the future depends on a multitude of factors, including nonlinear relationships between climate and population dynamics and the nature of altered disturbance regimes—all of which deserve future study. In conclusion, although the timing of compositional change is uncertain, and compositional change may continue to be slow in the near term, we believe that conservation biologists and resource managers should be prepared for large and potentially unpredictable changes in forests at Mount Rainier National Park as climate change becomes more severe.

Acknowledgments

We thank the many field assistants affiliated with the HilleRisLambers Lab and the Pacific Northwest Forest Permanent Sample Plot Network for collecting this valuable data, and R. Pabst for help in accessing and archiving the Pacific Northwest Forest Permanent Sample Plot Network Data. We thank Catherine Copass for providing us with legacy forest composition data from Mount Rainier National Park. We also thank Mt. Rainier National Park Staff for the opportunity to conduct this research, especially Regina Rochefort, Barbara Samora and Lou Whiteaker. Funding and data management for the Pacific Northwest Forest Permanent Sample Plot Network was provided by the US Forest Service Pacific Northwest Research Station, the Wind River Canopy Crane Research Facility, Oregon State University, and the HJ Andrews Experimental Forest LTER program. Funding for recruitment and tree ring work was provided by the UW Royalty Research Foundation (to JHRL), U.S. Department of Energy (DOE number DE-FC02-06ER64159 to JHRL) and the National Science Foundation (NSF Career DEB-1054012 to JHRL). Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of funding agencies.

Literature Cited

Acker, S. A., J. F. Franklin, S. E. Greene, T. B. Thomas, R. Van Pelt, and K. J. Bible. 2006. Two decades of stability and change in old-growth forest at Mount Rainier National Park. Northwest Science 80:65-72.

Acker, S. A., J. R. Boetsch, M. Bivin, L. Whiteaker, C. Cole, and T. Philippi. 2015. Recent tree mortality and recruitment in mature and old-growth forests in western Washington. Forest Ecology and Management 336:109-118.

Antos, J. A., R. Parish, and K. Conley. 2000. Age structure and growth of the tree-seedling bank in subalpine spruce-fir forests of south-central British Columbia. American Midland Naturalist 143:342-354.

Bates, D., and S. DebRoy. 2004. Linear mixed models and penalized least squares. Journal of Multivariate Analysis 91:1-17.

Bell, D. M., J. B. Bradford, and W. K. Lauenroth. 2014. Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. Global Ecology and Biogeography 23:168-180.

Bertrand, R., J. Lenoir, C. Piedallu, G. Riofrio-Dillon, P. de Ruffray, C. Vidal, J. Pierrat, and J. Gegout. 2011. Changes in plant community composition lag behind climate warming in lowland forests. Nature 479:517-520.

Bolker, B. M. 2008. Ecological models and data in R. Princeton University Press, Princeton, NJ.

Bonner, F., R. Karrfalt. 2008. The woody seed plant manual. United States Department of Agriculture, Washington, DC.

Brusca, R. C., J. F. Wiens, W. M. Meyer, J. Eble, K. Franklin, J. T. Overpeck, and W. Moore. 2013. Dramatic response to climate change in the Southwest: Robert Whittaker's 1963 Arizona Mountain plant transect revisited. Ecology and Evolution 3:3307-3319.

Bunn, A. G. 2010. Statistical and visual crossdating in R using the dplR library. Dendrochronologia 28:251-258.

Burns, R. M., B. H. Honkala. 1990. Silvics of North America: Conifers. Department of Agriculture, Forest Service, Washington DC.

Chen, I., J. K. Hill, R. Ohlemueller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333:1024-1026.

Cook, E. R., and K. Peters. 1981. The smoothing spline: A new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. Tree Ring Bulletin 41:43-53.

Cwynar, L. 1987. Fire and the forest history of the North Cascade range. Ecology 68:791-802.

Dalton, M. M., P. W. Mote, and A. K. Snover. 2013. Climate change in the Northwest: Implications for our landscapes, waters and communities. Island Press, Washington DC.

Daly, C., M. Halbleib, J. I. Smith, W. P. Gibson, M. K. Doggett, G. H. Taylor, J. Curtis, and P. P. Pasteris. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. International Journal of Climatology 28:2031-2064.

Damschen, E. I., S. Harrison, and J. B. Grace. 2010. Climate change effects on an endemic-rich edaphic flora: resurveying Robert H. Whittaker's Siskiyou sites (Oregon, USA). Ecology 91:3609-3619.

Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. Science 292:673-679.

De Frenne, P., F. Rodriguez-Sanchez, D. A. Coomes, L. Baeten, G. Verstraeten, M. Vellend, M. Bernhardt-Roemermann, C. D. Brown, J. Brunet, J. Cornelis, G. M. Decocq, H. Dierschke, O. Eriksson, F. S. Gilliam, R. Hedl, T. Heinken, M. Hermy, P. Hommel, M. A. Jenkins, D. L. Kelly, K. J. Kirby, F. J. G. Mitchell, T. Naaf, M. Newman, G. Peterken, P. Petrik, J. Schultz, G. Sonnier, H. Van Calster, D. M. Waller, G. Walther, P. S. White, K. D. Woods, M. Wulf, B. J. Graae, and K. Verheyen. 2013. Microclimate moderates plant responses to macroclimate warming. Proceedings of the National Academy of Sciences of the United States of America 110:18561-18565.

Devine, W., C. Aubry, A. Bower, J. Miller, and N. Maggiulli Ahr. 2012. Climate change and forest trees in the Pacific Northwest:a vulnerability assessment and recommended actions for national forests. U.S. Department of Agriculture, Olympia, WA.

Doak, D. F., and W. F. Morris. 2010. Demographic compensation and tipping points in climate-induced range shifts. Nature 467:959-962.

Dunwiddie, P. W. 1986. A 6000-Year Record of Forest History on Mount-Rainier, Washington. Ecology 67:58-68.

Ettinger, A. K., and J. HilleRisLambers. 2013. Climate isn't everything: competitive interactions and variation by life stage will also affect range shifts in a warming world. American Journal of Botany 100:1-12.

Ettinger, A. K., K. R. Ford, and J. HilleRisLambers. 2011. Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. Ecology 92:1323-1331.

Fisichelli, N., A. Wright, K. Rice, A. Mau, C. Buschena, and P. B. Reich. 2014. First-year seedlings and climate change: species-specific responses of 15 North American tree species. Oikos 123:1331-1340.

Ford, K. R., A. K. Ettinger, J. D. Lundquist, M. S. Raleigh, and J. HilleRisLambers. 2013. Spatial heterogeneity in ecologically important climate variables at coarse and fine spatial scales. Plos One 8:e65008.

Franklin, J. F., W. H. Moir, M. A. Hemstrom, S. E. Greene, and B. G. Smith. 1988. The Forest Communities of Mount Rainier National Park. US Department of the Interior, National Park Service, Portland, OR.

Franklin, J. F., F. J. Swanson, M. E. Harmon, D. A. Perry, T. A. Spies, V. H. Dale, A. Mckee, W. K. Ferrell, J. E. Means, S. V. Gregory, J. D. Lattin, T. D. Schowalter, and D. Larsen. 1991. Effects of global climatic change on forests in Northwestern North-America. Northwest Environmental Journal 7:233-254.

Gavin, D. G., and F. S. Hu. 2006. Spatial variation of climatic and non-climatic controls on species distribution: the range limit of Tsuga heterophylla. Journal of Biogeography 33:1384-1396.

Gavin, D. G., L. B. Brubaker, and D. N. Greenwald. 2013. Postglacial climate and fire-mediated vegetation change on the western Olympic Peninsula, Washington (USA). Ecological Monographs 83:471-489.

Gavin, D., J. McLachlan, L. Brubaker, and K. Young. 2001. Postglacial history of subalpine forests, Olympic Peninsula, Washington, USA. Holocene 11:177-188.

Hampe, A., and A. S. Jump. 2011. Climate relicts: Past, present, future. Annual Review of Ecology, Evolution, and Systematics 42:313-333.

Harrison, S., E. I. Damschen, and J. B. Grace. 2010. Ecological contingency in the effects of climatic warming on forest herb communities. Proceedings of the National Academy of Sciences of the United States of America 107:19362-19367.

Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology Letters 12:1040-1049.

Hemstrom, M. A., and J. F. Franklin. 1982. Fire and other disturbances of the forests in Mount Rainier National Park. Quaternary Research 18:32-51.

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

Kroiss, S. J., and J. HilleRisLambers. 2015. The importance of recruitment and microsite limitation for conifer regeneration in a warming world. Ecology:1286-1297.

Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T. Ebata, and L. Safranyik. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452:987-990.

Larson, A. J., and J. F. Franklin. 2010. The tree mortality regime in temperate old-growth coniferous forests: the role of physical damage. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 40:2091-2013.

Legendre, P., L. Legendre. 2012. Numerical Ecology. Elsevier, New York, NY.

Littell, J. S., E. E. Oneil, D. McKenzie, J. A. Hicke, J. A. Lutz, R. A. Norheim, and M. M. Elsner. 2010. Forest ecosystems, disturbance, and climatic change in Washington State, USA. Climatic Change 102:129-158.

Lutz, J. A., A. J. Larson, J. A. Freund, M. E. Swanson, and K. J. Bible. 2013. The importance of large diameter trees to forest structural heterogeneity. Plos One 8:e82784.

Lutz, J. A., A. J. Larson, T. J. Furniss, D. C. Donato, J. A. Freund, M. E. Swanson, K. J. Bible, J. Chen, and J. F. Franklin. 2014. Spatially non-random tree mortality and ingrowth maintain equilibrium pattern in an old-growth Pseudotsuga-Tsuga forest. Ecology 95:2047-2054.

McKenzie, D., Z. Gedalof, D. Peterson, and P. Mote. 2004. Climatic change, wildfire, and conservation. Conservation Biology 18:890-902.

McLachlan, J. S., and L. B. Brubaker. 1995. Local and regional vegetation change on the Northeastern Olympic Peninsula during the Holocene. Canadian Journal of Botany-Revue Canadienne De Botanique 73:1618-1627.

Merow, C., A. M. Latimer, A. M. Wilson, S. M. McMahon, A. G. Rebelo, and J. A. Silander Jr. 2014. On using integral projection models to generate demographically driven predictions of species' distributions: development and validation using sparse data. Ecography 37:1167-1183.

Okland, R. 1999. On the variation explained by ordination and constrained ordination axes. Journal of Vegetation Science 10:131-136.

Parish, R., and J. A. Antos. 2005. Advanced regeneration and seedling establishment in small cutblocks in high-elevation spruce-fir forest at Sicamous Creek, southern British Columbia. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 35:1877-1888.

Parish, R., and J. A. Antos. 2004. Structure and dynamics of an ancient montane forest in coastal British Columbia. Oecologia 141:562-576.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics 37:637-669.

Pederson, G. T., S. T. Gray, C. A. Woodhouse, J. L. Betancourt, D. B. Fagre, J. S. Littell, E. Watson, B. H. Luckman, and L. J. Graumlich. 2011. The unusual nature of recent snowpack declines in the North American Cordillera. Science 333:332-335.

R Core Team. 2015. R: A Language and Environment for Statistical Computing. Vienna, Austria.

Raleigh, M. S., C. C. Landry, M. Hayashi, W. L. Quinton, and J. D. Lundquist. 2013. Approximating snow surface temperature from standard temperature and humidity data: New possibilities for snow model and remote sensing evaluation. Water Resources Research 49:8053-8069.

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

Stewart, G. H. 1986. Population dynamics of a montane conifer forest, Western Cascade Range, Oregon, USA. Ecology 67:534-544.

Stueve, K. M., D. L. Cerney, R. M. Rochefort, and L. L. Kurth. 2009. Post-fire tree establishment patterns at the alpine treeline ecotone: Mount Rainier National Park, Washington, USA. Journal of Vegetation Science 20:107-120.

Svenning, J., and F. Skov. 2007. Ice age legacies in the geographical distribution of tree species richness in Europe. Global Ecology and Biogeography 16:234-245.

Svenning, J., S. Normand, and F. Skov. 2008. Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. Ecography 31:316-326.

Ter Braak, C. J. F. 1986. Canonical correspondence analysis—a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167-1179.

van Mantgem, P. J., J. C. B. Nesmith, M. Keifer, E. E. Knapp, A. Flint, and L. Flint. 2013. Climatic stress increases forest fire severity across the western United States. Ecology Letters 16:1151-1156.

van Mantgem, P. J., N. L. Stephenson, J. C. Byrne, L. D. Daniels, J. F. Franklin, P. Z. Fule, M. E. Harmon, A. J. Larson, J. M. Smith, A. H. Taylor, and T. T. Veblen. 2009. Widespread increase of tree mortality rates in the Western United States. Science 323:521-524.

von Arx, G., E. G. Pannatier, A. Thimonier, and M. Rebetez. 2013. Microclimate in forests with varying leaf area index and soil moisture: potential implications for seedling establishment in a changing climate. Journal of Ecology 101:1201-1213.

Weed, A. S., M. P. Ayres, and J. A. Hicke. 2013. Consequences of climate change for biotic disturbances in North American forests. Ecological Monographs 83:441-470.

Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. Frontiers in Ecology and the Environment 5:475-482.

Wyckoff, P. H., and J. S. Clark. 2002. The relationship between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains. Journal of Ecology 90:604-615.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Savaliev, and G. M. Smith. 2009. Mixed Effects Models and Extensions in Ecology With R. Springer, New York, NY.

Received 25 June 2014
Accepted 26 August 2015

Appendix A. Description of data types used from each of the 13 sites (see Fig. 2 for locations).

Site / Location (Fig. 2)	Objective 1[1,2,3] (vital rates at range limits)	Objective 2[4,5] (climate sensitivity)	Objective 3[6] (community turnover)
A (TO04)	Yes (mortality of TSHE, ABAM)	yes (germination)	yes
B (TB13)	Yes (mortality of THPL, PSME)	yes (germination)	no
C (AX15)	No	yes (germination)	no
D (AG05)	No	yes (germination)	yes
E (AV06)	No	yes (germination, tree growth of PSME, THPL)	yes
F (AM16)	Yes (germinant density of PSME, THPL & TSHE; sapling growth of TSHE; mortality of CANO & TSHE)	yes (germination, tree growth of TSHE)	yes
G (AR07)	Yes (germinant density of PSME, THPL & TSHE)	yes (germination)	yes
H (AE10)	Yes (germinant density of PSME, THPL & TSHE)	yes (germination)	yes
I (PARA)	Yes (germinant density of ABAM, CANO, PSME, THPL, TSHE, TSME; sapling growth of ABAM & TSME)	yes (germination, tree growth of ABAM, CANO, TSME)	no
J - M	no	yes (tree growth of ABLA)	no

1: germinant density based on 6 1m^2 plots surveyed over five years at each site.
2: sapling growth based on 20 individuals sampled at each site.
3: mortality based on 7 censuses conducted between 1978 and 2013 in 100 x100 meter stands
4: snow duration and soil moisture effects on germination based on 6 1m^2 plots surveyed over five years at each site, with snow duration and soil moisture measured within each plot annually.
5: snow duration and growing degree day effects on tree growth based on 20 cores collected per site per species.
6: community composition based on basal area change between 1978 and 2013 of 100 x100 meter stands (with all trees > 15 cm dbh monitored).

Appendix B. Estimated lower, mid and upper elevational ranges, based on the 463 forest plots surveyed between 1976–1980 (Franklin et al. 1988).

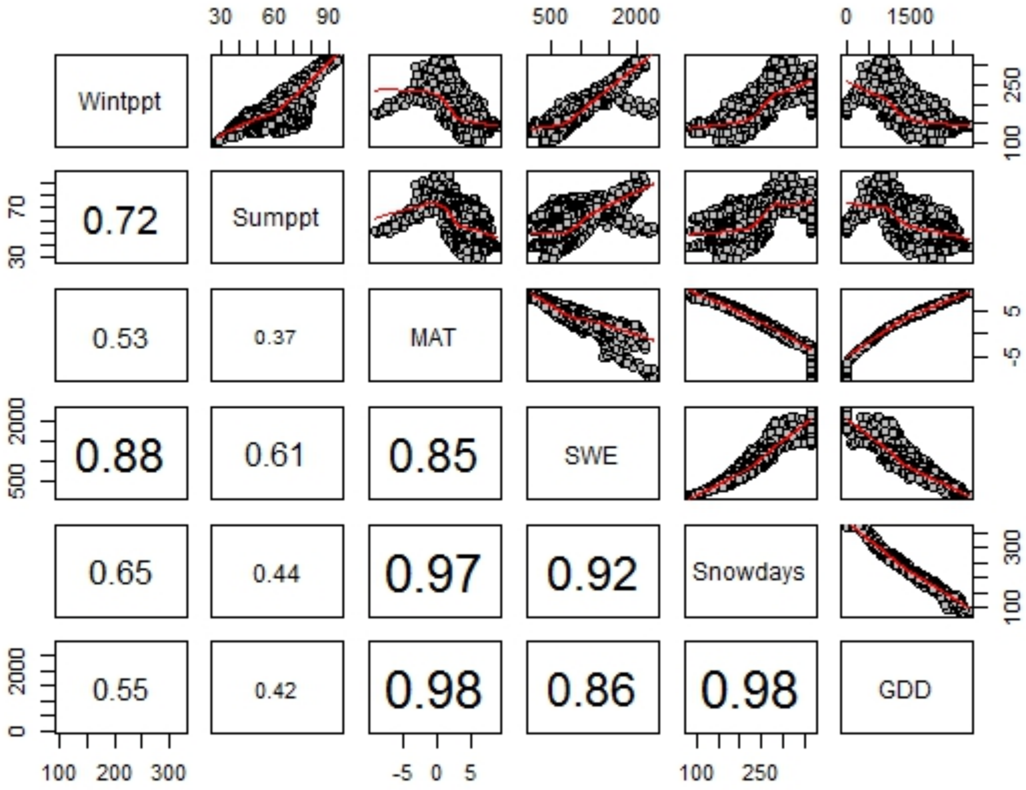
Species name	Lower third	Middle (core)	Upper third
Abies amabilis	542-992 m	992 – 1442 m	1442 – 1893 m
Callitropsis nootkatensis	835 – 1146 m	1146 – 1456 m	1456 – 1767 m
Pseudotsuga menziesii[1]	NA	542 – 1075 m	1075 – 1609 m
Thuja plicata[1]	NA	542 – 956 m	956 – 1369 m
Tsuga heterophylla[1]	NA	542 – 1075 m	1075 – 1609 m
Tsuga mertensiana	835 – 1162 m	1162 – 1490 m	1490 – 1817 m

1: These species are commonly found at lower elevations in the state of Washington. The lowest elevation of Mt. Rainier National Park is ~540 meters.

Appendix C. Sixteen tree species found in the 463 circular plots used to assess forest communities in 1978. Species also found in the six permanent forest stands are bolded.

4 Letter Code	Species name
ABAM	*Abies amabilis*
ABGR	*Abies grandis*
ABLA	*Abies lasiocarpa*
ABPR	*Abies procera*
ALRU	*Alnus rubens*
CANO	*Callitropsis nootkatensis*
PIAL	*Pinus albicaulis*
PICO	*Pinus contorta*
PIEN	*Picea engelmanii*
PIMO	*Pinus monticola*
PISI	*Picea sitchensis*
POTR	*Populus tremuloides*
PSME	*Pseudotsuga menziesii*
THPL	*Thuja plicata*
TSHE	*Tsuga heterophylla*
TSME	*Tsuga mertensiana*

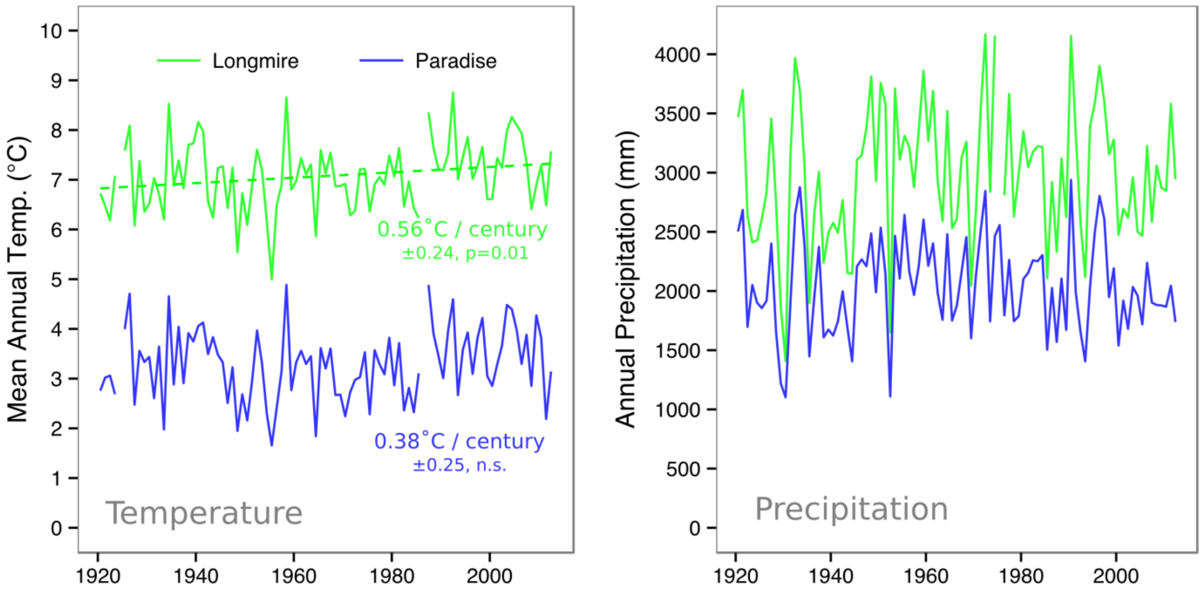
Appendix D. Correlations among climatic factors that vary spatially within Mt. Rainier National Park; including winter precipitation (Wintppt—cm precipitation between October and March), Summer precipitation (Sumppt—cm precipitation falling between June and August), mean annual temperature (MAT—in Celsius), snow pack (SWE—cm snow in water equivalent), snow duration (Snowdays—number of days the ground is covered by snow) and growing degree days (GDD, number of hours above 5 °C) across Mt. Rainier National Park. Gray points represent annual means from 30 year climate normals (1971–2000) on the right side, and correlations (Pearsons *r*) are shown in boxes on the left (with text scaled in size according to the strength of correlation between climate factors).



Appendix E. Basal area change in six old growth stands (over a 35 year time period).

Stand	Species	Basal area (cm^2 / m^2)				Turnover	
		1978 total	Growth (1978-2013)	Ingrowth (1978-2013)	Death (1978-2013)	New^{2013} / Total^{2013}	Dead^{2013}/ Total^{1978}
AE10	ABAM	48.382	8.917	0.403	5.837	0.180	0.121
	CANO	38.647	5.851	0.153	2.91	0.144	0.075
	TSME	2.266	0.343	0.037	0.52	0.179	0.229
	All	89.295	15.111	0.593	9.266	0.164	0.104
AR07	ABAM	30.601	2.602	0	8.951	0.107	0.293
	CANO	19.837	3.61	0.077	2.12	0.172	0.107
	TSME	27.729	4.42	0.076	0.086	0.140	0.003
	ALL	78.167	10.632	0.153	11.157	0.138	0.143
AM16	ABAM	12.122	3.684	1.187	1.778	0.32	0.147
	CANO	20.146	2.599	0.132	3.774	0.143	0.187
	TSHE	9.256	1.644	0.256	1.034	0.188	0.112
	TSME	19.027	2.18	0.216	2.951	0.13	0.155
	ALL	60.551	10.106	1.792	9.537	0.189	0.158
AV06	ABAM	21.247	7.938	2.184	8.517	0.443	0.401
	CANO	0.37	0.253	0	0	0.406	0
	PSME	6.465	0.716	0	0	0.100	0
	THPL	1.959	0.781	0	0	0.285	0
	TSHE	15.906	6.608	1.644	6.865	0.477	0.432
	ALL	45.947	16.295	3.828	15.383	0.397	0.335
AG05	ABAM	28.267	6.391	0.419	10.49	0.277	0.371
	PSME	20.905	2.374	0	0	0.102	0
	THPL	22.133	6.319	0.019	1.292	0.233	0.058
	TSHE	7.364	2.558	1.257	2.057	0.418	0.279
	ALL	78.669	17.642	1.695	13.839	0.230	0.176
TO04	ABAM	0.537	0.804	0.506	0.498	0.971	0.927
	PSME	17.586	2.588	0	3.176	0.152	0.181
	THPL	13.758	5.487	0	1.488	0.309	0.108
	TSHE	32.382	14.484	1.53	18.123	0.529	0.56
	ALL	64.263	23.362	2.036	23.285	0.383	0.362

Appendix F. Trends in Summer temperature and winter precipitation at two climate stations within Mt. Rainier national Park: Longmire (green) and Paradise (blue). Temperature records are monthly quality-controlled and homogenized values from the Berkeley Earth dataset (http://www.berkelyearth.org, Rohde et al. 2013) downloaded on March 18th 2014. Monthly precipitation data was aggregated from daily values downloaded from the Global Historical Climatology network (http://www.ncdc.noaa.gov/oa/climate/ghcn-daily/) on March 17th, 2014. Precipitation data was quality-controlled, and, in-line with the Berkeley Earth methodology, empirical change-point analysis (Chen and Gupta 2000) was used to detect long-term statistical departures from regional averages which probably represent station moves or sensor changes. Changepoint detection and bias adjustment was performed in R 2.15.1 using the package "changepoint" (Killick et al. 2014). We used the function "cpt.meanvar" to detect the location and optimal number of changepoints using the bin-segmentaton algorithm (Scott and Knott 1974), and the SIC penalty. Bias in precipitation measurements relative to the regional expectation was then assessed and corrected independently for each identified segment.



Literature for Temperature & Precipitation Trend Analyses (Appendix E)

Chen, J. and A. K. Gupta. 2000. Parametric statistical change point analysis. Birkhauser (Springer-Verlag), New York.

Scott, A. J. and M. Knott. 1974. A cluster analysis method for grouping means in the analysis of variance. Biometrics 30:507-512.

Killick, R. and I. Eckley. 2014. Changepoint: An R package for changepoint analysis. R package version 1.1.1. http://CRAN.R-project.org/package=changepoint

Rohde, R., R. Muller, R. Jacobsen, S. Perlmutter, A. Rosenfeld, J. Wurtele, J. Curry, C. Wickham, and S. Mosher. 2013. Berkeley earth temperature averaging process, Geoinformation & Geostatistics: An overview. 1:1-2.