

THESIS

TOPOGRAPHY, DISTURBANCE AND CLIMATE: SUBALPINE FOREST CHANGE 1972-
2013, ROCKY MOUNTAIN NATIONAL PARK, USA

Submitted by

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Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Spring 2015

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ABSTRACT

TOPOGRAPHY, DISTURBANCE AND CLIMATE: SUBALPINE FOREST CHANGE 1972-2013, ROCKY MOUNTAIN NATIONAL PARK, USA

Many forest tree species are expected to migrate in order to track suitable habitat due to changing climate (Stohlgren et al. 2000, Holzinger et al. 2007, Bell et al. 2013). Changes in climate will likely alter important fine-scale ecological factors such as water balance or microsite conditions which are vital for vegetation (Dobrowski 2011). Species distribution models suggest that many species should have already begun to migrate to track apposite climate (Rehfeldt et al. 2006, Littell et al. 2010, Monahan et al. 2013). While these models are a good starting point, they do not incorporate many variables that are critical for understanding forest changes and migration such as fine-scale topography and disturbance (Pearson and Dawson 2003). I resampled 68 subalpine forest plots originally surveyed in 1972-73 in Rocky Mountain National Park (RMNP) to investigate changes in species composition and structure and assess species migration during the past 40 years. I specifically considered forest change and migration in the context of topography, disturbance and climate. Data indicate species composition has remained relatively stable, with new species arriving in only 13% of plots. Forest structure has changed, shifting toward greater abundance of large-diameter trees with a reduction in small-diameter trees. Total stem densities decreased on south-facing slopes, increased on north-facing slopes, and remained stable at low elevations and increased at higher elevations. Species migration has been predominantly upslope on south-facing slopes while species elevations remained stable across north-facing slopes. These findings suggest that climate change has impacted forests of RMNP during the past 40 years. Impacts to vegetation have been mediated by topographic position and

disturbance, demonstrating the importance of these factors in altering climate change impacts at the microsite scale. Northern aspects appear to be more buffered from the impacts of warming temperatures than southern aspects and these areas may become potential refugia in the future. Further understanding of the interactions among topography, disturbance and climate is vital for anticipating how forests could change and this information will lead to better ecosystem management and preservation of biodiversity in the future.

ACKNOWLEDGEMENTS

I would like to thank the many people that contributed to this work and supported me along this journey. To my wife, Christina Esser, who stood by my side in the field many early summer mornings and supported me during all the high and low points along the way. Without the guidance and mentoring from Jason Sibold this project would not have been possible. Thanks to Ben Bobowski for providing this opportunity. The hard work of Carlyn Perovich who spent many nights in the backcountry resampling sites. The diligence of Tom Westcot and Allison Franz for their countless hours of data entry. Bill Monahan for his help with climate data and interpretations and Ben Baldwin for his constant humor and support.

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Introduction

Twenty-first century projected climate change will force many forest species to migrate in order to track suitable climate conditions (Stohlgren et al. 2000, Holzinger et al. 2007, Allen et al. 2010, Bell et al. 2013). Warming temperatures and greater variability in precipitation will affect important ecological factors such as water balance or site temperature which influence species distributions (Dobrowski 2011). Based on recent climate conditions, species distribution models suggest that many species should have already begun to migrate to track appropriate climate (Rehfeldt et al. 2006, Littell et al. 2010, Monahan et al. 2013). Although these models have proven valuable for illuminating recent climate effects on species distributions and for projecting future changes, they do not incorporate many variables that are critical in determining species distribution and migration (Pearson and Dawson 2003). For example, models do not include the influences of fine-scale topography or ecological disturbance (Overpeck et al. 1990, Pearson and Dawson 2003), both of which can have significant influences on regeneration, migration potential and species distributions (Grubb 1977, Peet 1981, Veblen et al. 1991a, 1991b, Veblen 1992, Dobrowski 2011). Recent empirical studies of species distributions, which reflect the suite of real world influences on species distributions and migration, do not present a clear pattern as to how forest systems are responding to recent climate. Specifically, research has documented species are moving upslope as expected (Beckage et al. 2008, Lenoir et al. 2008, Bell et al. 2013), downslope against expectations (Crimmins et al. 2011), not changing distribution (Zhu et al. 2012), not moving but experiencing shifts in species dominance or community assemblages (Kelly and Goulden 2008), shifts in demography (van Mantgem et al. 2009, Lutz et al. 2009, Dolanc et al. 2013) and possible extinction of species due to habitat loss (Pearson and Dawson 2003, Ashcroft 2010).

In mountainous terrain, climate change impacts on vegetation will be highly heterogeneous as a consequence of the significant influence that topography plays in creating microclimates (Peet 1981, Stephenson 1990, Dobrowski 2011). This connection between topography and climate has often been referred to as topoclimate (Thornwaite 1953) and can be critical to species regeneration or persistence at a site (Dobrowski 2011). In the northern hemisphere, north-facing slopes are associated with reduced solar radiation, which results in cooler temperatures, lower evapotranspiration rates and increased moisture availability. The opposite is true for south-facing slopes due to higher solar radiation. Moreover, elevation-temperature and elevation-solar radiation relationships create steep temperature gradients over short distances in mountain areas due to low heat holding capacity of the thin air (Keppel et al. 2012, Bach and Price 2013). Microclimates are essential to the regeneration and distribution of tree species and are controlled by a variety of variables such as aspect, elevation, slope and canopy cover. The effect of fine-scale topography on regional climate at the microsite level is not well documented. These effects could either attenuate regional climate trends creating potential refugia allowing species to persist or exacerbate regional climate trends forcing species to migrate (Ashcroft 2010, Dobrowski 2011, Moritz and Agudo 2013).

Natural ecological disturbances, in combination with climate and topography, play a critical role in shaping the composition, structure and regeneration of forest ecosystems (Grubb 1977, White 1979, Veblen et al. 1991a). Disturbance type, severity and extent creates very specific microsite conditions and generate the context for the degree of climate change at a site (Peet 1988, Veblen et al. 1991a). For example, stand-replacing fire exposes bare mineral soil and increases soil nutrients, creating very specific microsite conditions for regeneration. Removal of the canopy further alters microsite conditions by increasing wind and solar radiation. These

conditions promote stand regeneration of early successional species such as pines and aspen (Peet 1988, Veblen 1992). In contrast to fire, insect outbreaks that generally kill half or more of canopy trees create very different microsite conditions for regeneration. In these sites bare mineral soil is relatively rare and because insects are generally species-specific, shade from live non-host canopy trees is still present (Veblen et al. 1991a, Raffa et al. 2008, Collins et al. 2011). These conditions tend to promote regeneration of shade tolerant species and growth releases of advanced regeneration (Diskin and Rocca 2011, Collins et al. 2011). Thus, type and severity of disturbance create microsite conditions that can favor regeneration of one species over another and alter the successional trajectory of a stand (Grubb 1977, White 1979).

Numerous studies investigating species migration and forest change due to changes in climate have been conducted in Europe (Holzinger et al. 2007, Lenoir et al. 2008, Chen et al. 2011) and along the east and west coasts of the United States (U.S.) (Ibáñez et al. 2008, Beckage et al. 2008, Kelly and Goulden 2008, Crimmins et al. 2011). To date, there is a paucity of information on recent forest change and migration in the continental U.S. and few, if any, studies look at the influence of topography and disturbance as mediating factors of change. This study focused on investigating forest change and tree migration over the past 40 years in the context of topography, disturbance and climate in Rocky Mountain National Park, Colorado. I hypothesize that forest response to climate change is influenced at a local scale by topography and disturbance. I explored the variation of this response by measuring forest structure, composition and species migration and I address whether species have responded consistently on north versus south-facing slopes after 40 years and how this response varies by elevation and species.

Methods

Study Area

Rocky Mountain National Park (RMNP) straddles the continental divide in north-central Colorado (Figure 1). The area has been shaped by long-term geologic processes that have resulted in poorly developed soils and highly-dissected, steep topography. This topography creates a mosaic of climatic and environmental gradients from sheltered valley bottoms to exposed mountain summits, yielding a diverse set of ecosystems (Peet 1981). Three life zones (montane, subalpine, tundra) classified by dominant vegetation communities are located within RMNP (Marr 1961, Peet 1981). This study is focused on the subalpine life zone which is the largest forested area within RMNP (45km²). Six dominant forest tree species include: *Abies lasiocarpa* (subalpine fir), *Picea engelmannii* (Engelmann spruce), *Pinus contorta* (lodgepole pine), *Pseudotsuga menziesii* var. *menziesii* (Douglas-fir), *Populus tremuloides* (aspen) and *Pinus flexilis* (limber pine). These tree species generally promote a closed canopy system leading to minimal light reaching the forest floor, resulting in an understory composition that can be highly variable ranging from little to no understory species to highly diverse understory strata (Romme et al. 1986). In general, because of the high elevation and cooler temperatures, growing seasons are relatively short. The dominant disturbance types within these forests are infrequent stand-replacing fire, insect outbreaks and windthrow (Veblen and Donnegan 2006). Beginning in the early 2000s the study area experienced an epidemic mountain pine beetle outbreak (*Dendroctonus ponderosae*, MPB) resulting in extensive mortality of the preferred host trees, lodgepole pine and limber pine (Raffa et al. 2008, Coop and Schoettle 2009, Diskin and Rocca 2011, Edburg et al. 2012). Over the past few decades, spruce beetle (*Dendroctonus rufipennis* Kirby) and Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) have also caused severe

mortality of spruce and Douglas-fir (Veblen and Lorenz 1991, Veblen et al. 1991b, 1994, Veblen 2003, Veblen and Donnegan 2006). In the 1940s a large spruce beetle outbreak killed most canopy Engelmann spruce trees within central and northwestern Colorado (Veblen et al. 1991b). During the 1950s, and again in the 1980s, Douglas-fir beetle outbreaks killed vast amounts of large-diameter Douglas-fir trees throughout RMNP (Hadley 1994). Infrequent stand-replacing fire has also impacted subalpine forest systems of RMNP for the past several centuries. Infrequent fires occur on the order of every 200 to 800 years depending on forest cover type, creating a patchwork of uneven aged forests across the landscape (Sibold et al. 2006).

I resampled plots ($n = 68$) located in the lowest elevation montane/subalpine transition zone through the subalpine along the eastern slope of the continental divide in RMNP. Plot elevations spanned from 2618 m to 3566 m. Stand ages ranged from <100 years to >400 years old ($\bar{x} = 253$ years) and were obtained from previous fire history research (Sibold et al. 2006) and tree cores taken during the 1972 sampling (Peet 1975). Climate for the study area was acquired from parameter-elevation regression on independent slopes model (PRISM) at 4-km resolution between 1895-2013 (Figure 1; PRISM Climate Group, Oregon State University). Four locations were selected to represent main clusters of sites resampled. No sites are outside of a 10 km radius from the nearest climate location. Each climate location was located within an individual 4 km grid cell and was separated by an average of 12 km in order to represent the entire study area. Minimum mean annual temperature has risen considerably over the time period (T_{min} ; $\beta = 0.026$, $t = 14.38$, $R^2 = 0.6386$, $P = <0.0001$; Figure 2). Maximum mean annual temperature has also risen though at a slower rate than T_{min} (T_{max} ; $\beta = 0.0142$, $t = 7.29$, $R^2 = 0.3126$, $P = <0.0001$; Figure 2). Mean annual precipitation has been highly variable and does not

indicate a specific trend, although several droughts and wet periods have occurred ($\beta = 0.0047$, $t = 0.18$, $R^2 = 0.0003$, $P = 0.8588$; Figure 3).

Field Methods 1972-1973

Between 1972 and 1973, Dr. Robert Peet quantified forest conditions in 305 forest plots, of which 269 were located within RMNP. Plot locations were selected subjectively and placed within homogenous forest stands to ensure representation of a unique forest community (Peet 1981). The original goal was to determine drivers of forest community composition and structure patterns. Peet (1981) found that forests could be characterized along a moisture gradient which was influenced by various topographic features such as elevation, aspect and slope (Peet 1975, Peet 1981; Figure 4). Plots were one-tenth hectare in size (20 m x 50 m; see Whittaker 1960) and species abundance data for the herbaceous, shrub and tree strata were collected. Landscape characteristics data such as slope, aspect, elevation, slope position, exposure, soil conditions (e.g. moisture/type) and rock cover were also collected at each location. Each plot location was also recorded on USGS topographic maps. Species and diameter at breast height (DBH; measured at 1.37 m height) were recorded for all trees (live and dead) greater than 10cm in height within each plot. Peet divided live tree data into three structure classes: seedlings (stems ≤ 2.54 cm), saplings (stems between 2.54cm-7.62cm) and trees (stems ≥ 7.62 cm). Tree data and original USGS topographic maps with site locations from the 1972 survey were provided by Dr. Peet (personal communications). Tree data are also available from VegBank online (www.vegbank.org). For more information on sampling procedures and plot identification, see Peet (1981).

I resampled a subset of the original 269 plots within RMNP during the summer of 2013. I selected plots across two topographic gradients: aspect and elevation, specifically, north-facing or south-facing aspects and high or low-elevation. North-facing aspects fell between 293 degrees and 67 degrees and south-facing aspects between 113 degrees and 247 degrees. High-elevation was considered above 3048m and low-elevation sites were below 3048m. This classification placed all low-elevation sites within the transition areas between montane and subalpine life zones.

Plots were not permanently marked, thus exact relocation was not possible. Using plot coordinates (latitude, longitude), the original topographic maps (USGS 7.5 minute quads) with plot locations, and landscape characteristic data recorded during the initial survey (Dr. Peet, personal communication), I was able to locate the general forest stands. In each location, I sampled three one-tenth hectare plots (each 20 m x 50 m) nearest the original location, as exact plot resampling was not possible. The two adjacent plots were located no closer than 10m from any other plot edge. These methods decreased the influence of composition and structure variability across the landscape and between the two sampling events. Each three plot cluster was located within a half hectare area of the original forest plot. Due to a variety of landscape issues, such as abrupt aspect or slope change, the number of plots sampled in each cluster varied. Each plot was surveyed for trees using exact methods as Peet (1975, 1981) described above. To allow for relocation and future surveys, I captured accurate GPS coordinates at all 4 corners of each 2013 plot along with taking photos in each of the four cardinal directions from the center of each plot. For this study I used diameter classes to classify structure instead of Peet's categories (seedlings, saplings, trees) to better reflect size than estimated age of a tree. In general, small-

diameter trees are younger and large-diameter trees tend to be older. Diameter classes are grouped as follows: diameter class 1 (stems ≤ 2.54 cm; DC1), 2 (stems between 2.54cm-7.62cm; DC2) and 3 (stems ≥ 7.62 cm; DC3).

Analysis

Data from the three individual plots collected at each site were averaged to generate a 2013 dataset (sensu Minnich et al. 1995). Tree abundance data were grouped by diameter class (DC1, DC2 and DC3, see above) and total stem density was calculated for the entire plot and each species. Tree abundance data were normalized from the plot level (stems/plot) to the landscape scale (stems/ha) to match the format of the 1972 dataset. This allowed for direct comparison to determine temporal changes in forest structure.

Comparisons of forest structure changes between 2013 and 1972 datasets were made for individual species and plots for all diameter classes and total stem densities. To understand the role of topography, comparisons were made among plots and species classified by aspect and elevation. Comparisons based on group characteristics included testing north versus south-facing sites and high versus low-elevations. Changes in abundance between datasets were tested using the Wilcoxon-Signed-Rank non-parametric test ($H_0: \mu=0; \alpha=0.05$). A non-parametric test was chosen after Shapiro-Wilks tests indicated that assumptions of normality were not met (SAS statistical software version 9.3).

To determine whether species are migrating, I used changes in DC1 median elevation (m) between 1972 and 2013 as a proxy. The smallest diameter class was chosen as the best proxy for migration because small-trees are climate-sensitive and unable to tolerate climate fluctuations (sensu Zhu et al. 2014). Small-diameter trees also best represent spatial changes in the

regeneration niche, opposed to larger trees, as they likely germinated more recently. For example, a species that is migrating upslope would show an increase in median elevation of DC1 between 1972 and 2013. To establish migration direction, abundance of DC1 for each species across sampling year and aspect were calculated and weighted according to the associated plots elevation. To understand the role of topography in migration, the median elevation of DC1 for each species was compared for both north and south-facing slopes.

I examined the arrival of new species within plots to assess shifts in species composition. The arrival of new species to a site would demonstrate a clear compositional shift. Abundances of DC1 and DC2 were used as indicators of shifts in species composition to reduce the likelihood of including species that were un-sampled in the 1972 survey. This was important due to the inability of measuring exact locations. Species that did not get recorded during the original survey that are present in the 2013 survey within DC1 or DC2 were considered new to the site.

Results

Resampled Plots

I identified 83 sites from the original 269 sites that met the criteria of elevation and aspect for resampling. I resampled 68 of 83 sites during the summer of 2013 (Figure 1). Seventy-five percent of sites (51/68) had three contemporary plots sampled, 18% (12/68) had two contemporary plots sampled and 7% (5/68) had only one contemporary plot sampled. Upon relocation four sites were found within a large stand replacing fire that occurred in 1978 (Ouzel Fire) and one site was mechanically thinned in 2010 for fire mitigation near the park boundary. These five plots were excluded from all cumulative analyses. Nineteen plots had >10% of total stems killed by insects, primarily bark beetles.

Structure changes

Between 1972 and 2013, when all sites and all species are considered, stem densities changed in all diameter classes ($n = 63$). During the 40 year study period, total stem density within the landscape remained relatively stable increasing only 2% ($P = .1664$) with a shift towards greater abundance of large-diameter trees (Table 1; Figure 5). Small-diameter stems (DC1) decreased 13%, although differences were not significant between sampling events (DC1: 0-2.54cm; $P = 0.1222$; Table 1; Figure 5). Density of large-diameter stems (DC2 and DC3) increased over the study period, both of which differences were borderline significant (DC2: 2.54-7.62cm; 14%; $P = 0.0661$ and DC3: >7.62cm; 6%; $P = 0.0554$; Table 1; Figure 5).

Examining structure changes by species clearly shows a species-specific response. Small-diameter tree abundance decreased, but not significantly, for Engelmann spruce (-20%; $P = 0.2375$), lodgepole pine (-38%, $P = 0.0817$), aspen (-42%; $P = 0.1552$) and limber pine (-47%; $P = 0.0576$). Small-diameter tree abundance increased for subalpine fir (4.51%; $P = 0.9513$) and Douglas-fir (657%; $P = 0.0039$).

There was greater abundance in the number of diameter class 2 stems for all species except lodgepole pine. Lodgepole pine had significant decrease in abundance (-57%; $P = 0.0122$). Subalpine fir and aspen had significant increases over the 40 year period (72%; $P = <0.0001$ and 89%; $P = 0.0125$, respectively).

The abundance in the largest-diameter class (DC3) increased for all species except lodgepole pine (-24%; $P = 0.0147$). Four species differed significantly from their 1972 abundances: subalpine fir (55%; $P = <0.0001$), Engelmann spruce (21%; $P = 0.0005$), Douglas-fir (122%; $P = 0.0023$), and aspen (294%; $P = 0.0471$) (Table 1).

Total stem density of three species decreased: lodgepole pine, aspen and limber pine. Only lodgepole pine had significant decreases (-31%; $P = 0.0008$). The abundance of total stems of subalpine fir and Douglas-fir increased significantly (28%; $P = <0.0001$ and 224%; $P = 0.0174$ respectively). *Pinus ponderosa* (Ponderosa pine) was identified in two plots although densities were too low for statistical analyses (Table 1).

Structure changes across aspects

During the study period, stems densities varied between aspects for nearly all diameter classes. Total stem density on south-facing slopes ($n = 33$) has decreased by 8% ($P = .6493$, Figure 6). South-facing sites had a reduction in DC1 stem abundance which differed significantly from the 1972 survey (-36%; $P = 0.0081$). Abundance of diameter class 2 also declined (-4%; $P = 0.2298$), although differences were minor. Diameter class 3 had a slight increase in stems (3%; $P = 0.5576$).

In contrast, since 1972, total stem density on north-facing sites ($n = 30$) had a significant increase (8%, $P = 0.0344$; Figure 6). Diameter class 1 has remained comparatively stable with only a slight decrease of abundance (-3%; $P = 0.9441$). Diameter class 2 and 3 had greater abundance of stems (26%; $P = 0.049$ and 9%; $P = 0.0463$, respectively).

Structure change across elevation

Differences in stem abundance occurred within high and low-elevation sites and between sampling events. High-elevation sites ($>3048\text{m}$, $n = 24$) had increases in total stem density over the study period (8%; $P = 0.0661$; Figure 7). The abundance of DC1 decreased by 14% ($P = 0.0616$). Larger-diameter stems showed greater abundance with DC2 increasing 11% ($P = 0.0757$) and DC3 significantly increasing 22% ($P = 0.0041$) within high-elevation sites.

Low-elevation sites (<3048m, n = 39) had a 2% decline in total stem density (P = 0.6912; Figure 7). Diameter class 1 reduced in abundance by 13% (P = 0.540). Diameter class 2 was the only class to increase in abundance (16%; P = 0.2915). Diameter class 3 declined 2% (P = .6912) since 1972.

Species migration

During the past 40 years, changes in median elevations (in meters) of small-diameter trees (DC1) for north and south-facing slopes indicates species are migrating within RMNP. This migration has been highly dependent on topographic position. On south-facing slopes, species elevation changes generally denote movement upslope. Engelmann spruce, lodgepole pine, Douglas-fir and limber pine all had greater abundance of DC1 at higher elevation than in 1972 (\bar{x} = 86 m, range: 9 m – 280 m) with limber pine having the greatest change (280 m). Subalpine fir was the only species to migrate downslope on south-facing slopes, having increased abundance occurring at 25m lower than in 1972. Aspen elevations remained stable over the study period (Figure 8). On north-facing slopes, median elevation remained equal for subalpine fir, Engelmann spruce, Douglas-fir, aspen and limber pine. Lodgepole pine showed a slight decrease in elevation (5m; Figure 8).

Compositional changes

Species composition within all sites has remained relatively stable for the 40 year study period. Diameter class 1 was used as the indicator of new species arrival to a site. 13% of all plots had additional species that were not reported during the 1972 study, of which 75% were located on south-facing slopes and 68% were at low-elevations. Using DC2 as the indicator, 13%

of all plots had additional species that were not recorded during the 1972 study, of which 63% were located on north-facing slopes and 87% were at low-elevations.

Discussion

Subalpine forests of RMNP have changed significantly over the past 40 years, with evidence of both changes in forest structure and species migration. In general, forest structure has shifted towards increased abundance of large-diameter stems (DC2 and DC3) while small-diameter stems densities (DC1) have declined (Table 1; Figure 5, 6, 7). Special attention needs to be given when comparing the results of this study to previous research since similar terms are used to describe different size classifications (i.e., large vs small-diameters). The following studies refer to trees with 10cm-30.4cm DBH as the smallest size class. In this context, my results are similar to the majority of research assessing recent structure changes in the context of climate change from other forest systems. These studies found a shift towards greater abundance of small-sized trees (10cm-30.4cm) (Minnich et al. 1995, van Mantgem et al. 2009, Lutz et al. 2009, Dolanc et al. 2013). Results of this study indicate that species are migrating in response to recent climate shifts. The primary direction of migration is upslope on south-facing slopes and an overall lack of migration is occurring on north-facing slopes (Figure 8). Species migrations due to warming temperatures have been documented globally for a variety of species (Parmesan and Yohe 2003, Beckage et al. 2008, Kelly and Goulden 2008, Crimmins et al. 2011, Bell et al. 2013). However, none of this research has specifically studied migration in the context of topography or disturbance despite several studies emphasizing the importance of these factors (Ashcroft et al. 2007, 2009, Ashcroft 2010, Dobrowski 2011). In the case of RMNP, topography and disturbance appear to have played a central role in shaping subalpine forest response to recent climate change.

Topographic contingencies of forest change

Recent forest changes are strongly related to topographic position, with decreases in total stem densities on southern aspects and increases on northern aspects. These differing results likely reflect the influence of topography on microclimate and thus vegetation. The decrease in total stem density on south-facing slopes can be explained by the significant decrease in small-diameter trees that offset slight increases in density of larger stems (Figure 6). The increase in large-diameter stems on south-facing slopes was species-specific, with subalpine fir, Engelmann spruce, Douglas-fir and aspen increasing in density. The abundance of both pine species (*P. contorta* and *P. flexilis*) decreased. The decline in *Pinus* species has been documented elsewhere in the western U.S. and is primarily due to recent MPB outbreaks (Minnich et al. 1995, van Mantgem et al. 2009, Lutz et al. 2009, Dolanc et al. 2013, Coop et al. 2014). Forests on north-facing slopes are characterized by increased stem densities. On these slopes, large-diameter stems increase for all species, except lodgepole pine (Table 1, Figure 6). The density of small-diameter trees on north-facing slopes decreased when looking at all species combined. However, examining species-specific responses reveals the majority of species are increasing or stable in their small-diameter stem densities. Subalpine fir, lodgepole pine, Douglas-fir and aspen all increased on either north-facing or high-elevation sites. Coop et al. (2014) found similar patterns, documenting an overall reduction in small-live conifer stems (<2.5cm) since 1964 in aspen stands near Crested Butte, CO. The increased density of forests on north-facing slopes parallels results found in other studies from the western U.S. despite only one looking at the effects of aspect specifically. Several authors attributed longer growing seasons and fire suppression as the main reason for increased stem densities (Minnich et al. 1995, van Mantgem et al. 2009, Lutz et al. 2009, Dolanc et al. 2013). Fire suppression is not likely the main driver of increased stem

density found in this study since fire history research indicates that fire return intervals are within historic ranges of variability for lodgepole dominated forests (162-216 years) and spruce/fir forests (401-713 years) (Sibold et al. 2006). Warming temperatures and stable precipitation effects on growing season length could be a good explanation for the increased density of forests. The short growing season of the subalpine life zone was likely a limiting factor for vegetation, effecting regeneration, establishment and recruitment (Dolanc et al. 2013). An extension of the growing season on north-facing slopes may have allowed small-diameter stems to maintain their abundances while the longer growing season made conditions even drier on south-facing slopes.

Forest change in the context of topographic position (i.e., aspect and elevation) implies a connection between topographic complexity and the recent warming trend occurring in the study area. Topographic complexity acts as a filter, shaping climate change influences at a microsite scale. At this scale, topography influences variables, such as moisture availability, that are critical for vegetation survival and regeneration. Southern aspects receive more solar radiation throughout the year, amplifying the warming climate at these locations. This results in increased evapotranspiration and potentially earlier snowmelt, reducing water availability for vegetation, especially later in the growing season (Lutz et al. 2009, Bach and Price 2013). Research has shown snowmelt in RMNP is occurring 2-3 weeks earlier than in the late 1970s (Clow 2010). On north-facing slopes, topography may be ameliorating warming effects on vegetation as indicated by more stable patterns of regeneration and increased total stem density since the early 1970s. North-facing slopes receive lower amounts of solar radiation, which buffers against the influence of warming on soil moisture availability, either through evapotranspiration or snowpack dynamics. Furthermore, more dense vegetation, which is common on north-facing slopes, shades the forest floor, which further buffers the impact of warmer regional climate

trends (Lenoir et al. 2008). This has allowed for a more gradual warming effect on north-facing slopes compared to south-facing slopes. The decline in total stems, especially small-diameter stems, suggests south-facing slopes are becoming increasingly hot and dry. Northern aspects appear to be attenuating the effect of warming temperatures and reducing negative impacts for vegetation, whereas south-facing slopes are exacerbating the warming impacts on vegetation.

The importance of topography in mediating warming temperatures and forest change is also evident in patterns of species migration over the past 40 years. Small-sized trees (DC1) are the best indicator of migration because they likely germinated recently and thus reflect the suitability of a specific location for regeneration (i.e., regeneration niche, Grubb 1977). Furthermore, due to small-sized trees being less tolerant of climate extremes, their presence indicates suitable climate regimes (Zhu et al. 2014). On north-facing slopes, the elevational distribution of small-diameter trees is similar to the 1972 survey. This demonstrates an overall lack of species migration on these cooler/wetter slopes that are relatively buffered from warming temperatures. Zhu et al. (2012) found a similar lack of migration when looking at latitudinal changes, but did not investigate potential variability in species distributions in relation to topography. In contrast to north-facing slopes, current distributions of small-diameter trees on south-facing slopes indicate several species have migrated, predominantly upslope. Small-diameter Engelmann spruce, lodgepole pine, Douglas-fir and limber pine all have median elevations higher than in 1972. Several other studies have found an upslope migration of plant species (Parmesan and Yohe 2003, Holzinger et al. 2007, Beckage et al. 2008, Lenoir et al. 2008, Chen et al. 2011). Upslope migration of limber pine, may be particularly interesting since its distribution has already contracted significantly during the Holocene from increased competition, MPB mortality and white pine blister rust (*Cronartium ribicola*; Stohlgren et al. 2000). Further

upslope migration may lead to range contraction, which could jeopardize this species' persistence in the future. Whereas the majority of migration has been upslope, subalpine fir and lodgepole pine small-diameter distributions were lower than in 1972. Crimmins et al. (2011) found a downhill shift in species optimum elevation for various plant taxa of California. The authors attributed the downslope movement to increased precipitation during the growing season overriding warming temperatures. The stable precipitation patterns occurring across this study site (Figure 3) do not support precipitation changes as the driver of the downward shifts. Another factor potentially driving the downslope shifts is reduced competitive interaction created by the recent insect outbreaks killing large canopy trees (Lenoir et al. 2010). Reduced competition could likely be the best explanation for the downslope migration found in this study since 84% of sites experiencing insect outbreaks occurred at low-elevations (<3048m) allowing greater regeneration. Other authors have discussed the influence of cold air drainages driving downslope movement, although more research is needed to fully understand the role this plays (Dobrowski 2011). It seems evident from this research that understanding the connection between topographic position and climate change is critical to identifying locations of species migration in the future or whether a lag in migration is occurring.

Disturbance-mediated forest change

Disturbance has always been considered an important driver of forest change and succession. While the primary focus of this study was to look at forest change in the context of topographic position and recent climate change, many sites were disturbed between surveys. Several insect outbreaks occurred within RMNP during the 1980s and again in the early 2000s. A number of sites (n = 19) had >10% of the total trees killed by insects. Within these sites, Douglas-fir and aspen experienced a pulse of regeneration that was not documented in sites

without recent beetle activity. This pulse occurred on both south and north-facing slopes. North-facing slopes also had an increase in subalpine fir regeneration. The increase of these three species are similar to other MPB disturbance studies from the southern Rockies, which documented increases of subalpine fir and aspen following MPB outbreaks (Sibold et al. 2007, Diskin and Rocca 2011, Collins et al. 2011, Kulakowski et al. 2013, Coop et al. 2014). Subalpine fir and Douglas-fir are shade tolerant and able to germinate in organic matter (Hadley 1994), allowing them to take advantage of opportunities created in insect impacted forests. The semi-drought tolerance of Douglas-fir has likely facilitated this species to establish in the context of warming temperatures and recent drought. Subalpine fir only increased on north-facing slopes, taking advantage of the more stable soil moisture. Surprisingly, aspen abundance increased on both aspects despite its low tolerance to drought, high rates of elk browsing found within the park (Baker et al. 1997) and recent decline due to warming climate (Smith and Smith 2005, Anderegg et al. 2013, Coop et al. 2014). The increased abundance of aspen in the context of the recent bark beetle outbreaks probably reflects aspen's ability to re-sprout quickly from roots and take advantage of available resources and reduced competition. The reasons for decreased regeneration of other species in relation to the recent bark beetle outbreaks are not fully clear. Topographic position may have been a key driver in this decline. Forty-seven percent of beetle impacted sites were located on south-facing slopes and 53% on north-facing. South-facing slopes had a 36% and 24% decline in DC1 for disturbed and undisturbed sites, respectively. This demonstrates that disturbance had little impact on the overall pattern of decline in regeneration. The already less dense vegetation and increased mortality of large trees on south-facing slopes may have increased wind and provided less shade, affecting a site's evapotranspiration, snowpack retention and runoff rate (Pugh and Small 2012). The decrease in soil moisture and

greater soil loss from erosion associated with increased runoff could have been the limiting factors for tree regeneration. This scenario could explain the higher rate of reduction in small-diameter trees found in south-facing disturbed sites.

While species regeneration on south-facing slopes did not benefit from disturbance, species on north-facing slopes did benefit. This further supports the importance between the interaction of topography and disturbance. On north-facing sites, small-diameter stems increased 14% in disturbed sites while decreasing 5% in undisturbed sites. New canopy gaps and reduced competition, while being sheltered from effects of warming temperatures, allowed for greater increases in DC1. Furthermore, the greater release of advanced regeneration, evident by the 26% increase in medium-size trees (DC2) in post-beetle stands, is likely in response to greater moisture since advanced regeneration declined on south-facing slopes. More open canopies and reduced competition for light is often more effectively utilized by established vegetation (Veblen et al. 1991b). In a study from the southern Rockies, Collins et al. (2011) documented the doubling of growth in advanced regeneration in MPB disturbed sites.

The response of vegetation to the 1978 Ouzel fire further supports the important role of disturbance in shaping forests in a changing climate. If disturbance does in fact provide opportunities for adaptation to climate (Overpeck et al. 1990, Rehfeldt et al. 2006), post-fire forest regeneration and recruitment should consist of drought tolerant and lower elevation species. However, within the four sites resampled in the Ouzel fire, forests converted from a spruce-fir cover type to an aspen-lodgepole pine cover type, species that are adapted to regeneration in post-fire sites. Although this response to fire has been consistent in these systems for the past several millennia (Caffrey and Doerner 2012), persistence of aspen provides evidence for a subtle contradiction. While aspen suckers are abundant immediately following fire

(Kay 1993, Romme et al. 1995, Kulakowski et al. 2013, Coop et al. 2014), aspen has also been shown to be susceptible to greater mortality from increasing temperatures and drought (Anderegg et al. 2013). Within the Ouzel fire, aspen both prolifically re-sprouted and recruited to large-diameter classes, suggesting that warming temperatures and drought have not influenced post-fire regeneration or recruitment. Post-fire site conditions and species adaptations to fire may be more of a factor in determining species composition than climate. This is further supported since plots were located equally on north and south-facing slopes. While classic patterns of post-fire regeneration held true for the Ouzel fire, if temperatures continue to warm and drought becomes increasingly more frequent, this may not be the case in the future. More research on recent fires could help elucidate if this pattern will persist in the future.

Conclusions and Implications

Forest change over the past 40 years in RMNP indicates topographic position and disturbance appear to play important roles in shaping vegetation response in a changing climate. The overall decrease in small-diameter trees (i.e., regeneration) and skew towards large-diameter stems is particularly important for future forest preservation. Substantial differences in vegetation response between aspect and elevation clearly demonstrate the importance of topographic position on how recent warming and highly variable precipitation are impacting changes in vegetation. The notion that topographic position can either buffer or exacerbate recent changes in climate is further supported by the drastic difference in species migration between aspects. The lack of overall migration on northern aspects and overwhelmingly upslope migration documented on south-facing aspects distinctly illustrates the effects of topographic position in changing or maintaining habitat suitability. The spatial heterogeneity of topoclimate in mountainous terrain provides a variety of opportunities for vegetation to respond to climate

change. Mediation of water balance, evapotranspiration and soil moisture by topography appear to dictate regeneration patterns and whether species are able to persist in situ or are forced to migrate. Understanding the role of fine-scale topography in shaping climate change impacts on vegetation will be vital to understanding and anticipating future forest change. While topography seems to be a large driver in understanding forest change, the interactions of topography and disturbance are also important. Disturbance, especially in the context of topography, also plays a critical role in maintaining or creating opportunities for species to persist or migrate on the landscape. Current vegetation response to disturbance has remained consistent with historical responses in areas where the microclimate has not been altered such as on north-facing slopes. In areas where warming temperatures have not been buffered, disturbance has appeared to exaggerate warming effects, causing declines in vegetation.

This research has important management implications for the preservation of forest species biodiversity under changing climates. For instance, this study identifies variables that are important to detecting potential climate refugia, which have been integral in the preservation of species during several climate shifts since the last ice age (Ashcroft et al. 2009, Ashcroft 2010, Bell et al. 2013). These refugia will be an important component of biodiversity preservation in the coming century and without refugia species may be lost from the landscape entirely. Incorporating forest change information from fine-scale topography research into species distribution models could help refine model predictions. This could allow for better identification of refugia locations so they can be protected. Ultimately, this information will provide managers with more reliable information for decision making in the face of an uncertain future.

This study also provides information for better ecosystem management. The cascading effects of forest change on ecological processes and species interactions could be numerous and

hinder ecosystem function and cause loss of ecological services (Parmesan 2006). Understanding changes to forests is vitally important to maintaining ecological services such as water quality and ecological processes such as phenology. Decreased vegetation cover can alter the retention of snowpack, which increases or changes the timing of runoff. Earlier snowmelt could alter the timing of water availability to plants, affecting their phenological synchronies with pollinators or species that utilize them as food sources (Parmesan and Yohe 2003, Forrest and Miller-Rushing 2010, Moritz and Agudo 2013). Increased rates of runoff could affect water quality by increasing sediment inputs to streams (Clow and Sueker 2000, Clow 2010) and alter timing and duration of peak flows (Pugh and Small 2012).

It is becoming exceedingly difficult to manage forests undergoing rapid changes due to recent warming temperatures and highly variable precipitation patterns. Managers must be ready to make decisions with large amounts of uncertainty that have potential for unidentified cascading effects. To assist with this difficult task, Millar et al. (2007) offers three options for managing forests in the face of uncertainty. These options include: resistance, resilience and response. Resistance options attempt to manage against change or protect highly valued resources. Resiliency options attempt to build capacity of forest to return to previous condition after a perturbation and response options embrace change and assist transitions toward new systems. Response options have not been well received in wilderness areas since they often involve human manipulations such as facilitated migration. This leaves resiliency and resistance options as the most plausible. Currently, many federal agencies support the use of resiliency and resistance options and some aspects of these options have already been incorporated into service-wide climate change strategic planning (NPS 2010). The uncertainty of how climate change will unfold in the future may require managers to have a more open minded approach to change. This

will be especially important when considering politically sensitive issues, such as disturbance from fire and insect outbreaks, and the role they play in maintaining the resiliency of forests (Millar et al. 2007). The heterogeneity of vegetation response in the context of topography, disturbance and climate change demonstrates that policy alone cannot dictate management. This information should persuade managers to conduct scenario planning through looking at a suite of potential options and outcomes in order to meet their missions.

Tables and Figures

Table 1: Summaries for all species combined and seven individual species across all plots (n = 63) by diameter class. ABLA (*Abies lasiocarpa*), PICO (*Pinus contorta*), PIEN (*Picea engelmannii*), PIFL (*Pinus flexilis*), PIPO (*Pinus ponderosa*), POTR (*Populus tremuloides*), PSME (*Pseudotsuga menziesii*). DC1 (0-2.54cm), DC2 (2.54cm-7.62cm) and DC3 (>7.62cm). Significant changes noted in bold (P < 0.05).

		DC1	DC2	DC3	Total Stems
All Species Combined	Stems/ha 1972	1282.585	557.542	1324.293	3164.42
	Stems/ha 2013	1073.254	684.103	1447.459	3204.816
	Percent Change	-16.321	22.700	9.301	1.277
	P-value (Wilcoxon)	0.1222	0.0661	0.0554	0.1664
ABLA	Stems/ha 1972	485.179	155.714	181.786	822.679
	Stems/ha 2013	507.035	267.196	281.411	1055.642
	Percent Change	4.505	71.594	54.803	28.318
	P-value (Wilcoxon)	0.9513	<0.0001	<0.0001	<0.0001
PICO	Stems/ha 1972	71.957	167.826	674.783	914.566
	Stems/ha 2013	44.848	71.63	511.217	627.695
	Percent Change	-37.674	-57.319	-24.240	-31.367
	P-value (Wilcoxon)	0.0817	0.0122	0.0147	0.0008
PIEN	Stems/ha 1972	257.857	120.357	293.75	671.964
	Stems/ha 2013	205.107	130.911	355.482	691.5
	Percent Change	-20.457	8.769	21.015	2.907
	P-value (Wilcoxon)	0.2375	0.1068	0.0005	0.2386
PIFL	Stems/ha 1972	36.75	25.25	104	166
	Stems/ha 2013	19.525	25.4	113.925	158.85
	Percent Change	-46.871	0.594	9.543	-4.307
	P-value (Wilcoxon)	0.0576	0.0802	0.4052	0.6249
PIPO	Stems/ha 1972	0	0	8	8
	Stems/ha 2013	0	0.6	9.2	9.8
	Percent Change	0	0	15	22.5
	P-value (Wilcoxon)	0	1	1	1
POTR	Stems/ha 1972	424	80.5	22.5	527
	Stems/ha 2013	244.95	152.05	88.75	485.75
	Percent Change	-42.229	88.882	294.444	-7.827
	P-value (Wilcoxon)	0.1552	0.0125	0.0471	0.961
PSME	Stems/ha 1972	6.842	7.895	39.474	54.211
	Stems/ha 2013	51.789	36.316	87.474	175.579
	Percent Change	656.928	359.987	121.599	223.881
	P-value (Wilcoxon)	0.0039	0.0603	0.0023	0.0174

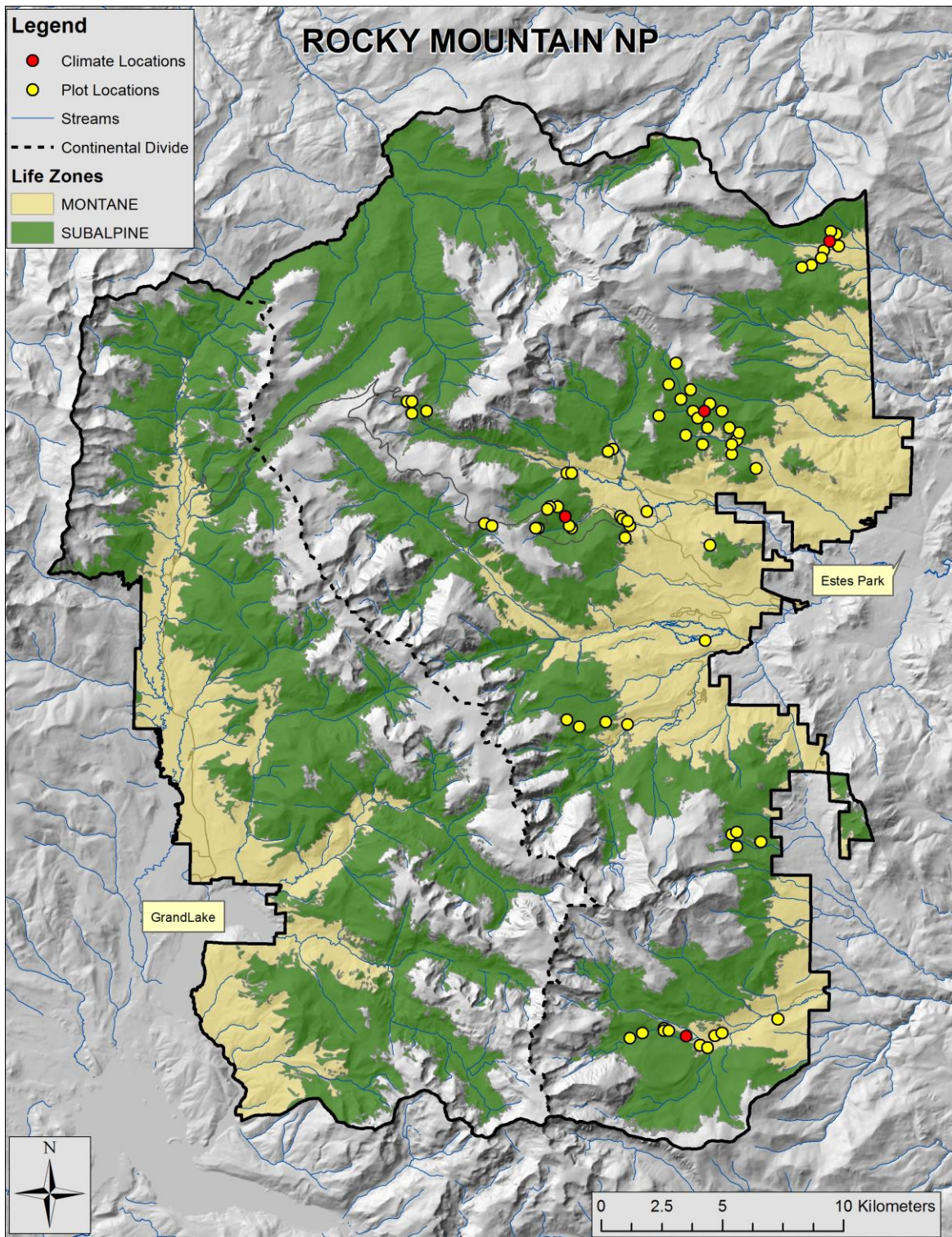


Figure 1: Map showing all 68 sites sampled by Peet (1972) and resampled in 2013 (yellow points) within Rocky Mountain National Park. Red points indicate locations where PRISM climate was downloaded. Within the park boundary green shaded area is subalpine forest, beige is montane forest and grey is unforested.

Mean Annual Maximum and Minimum Temperature

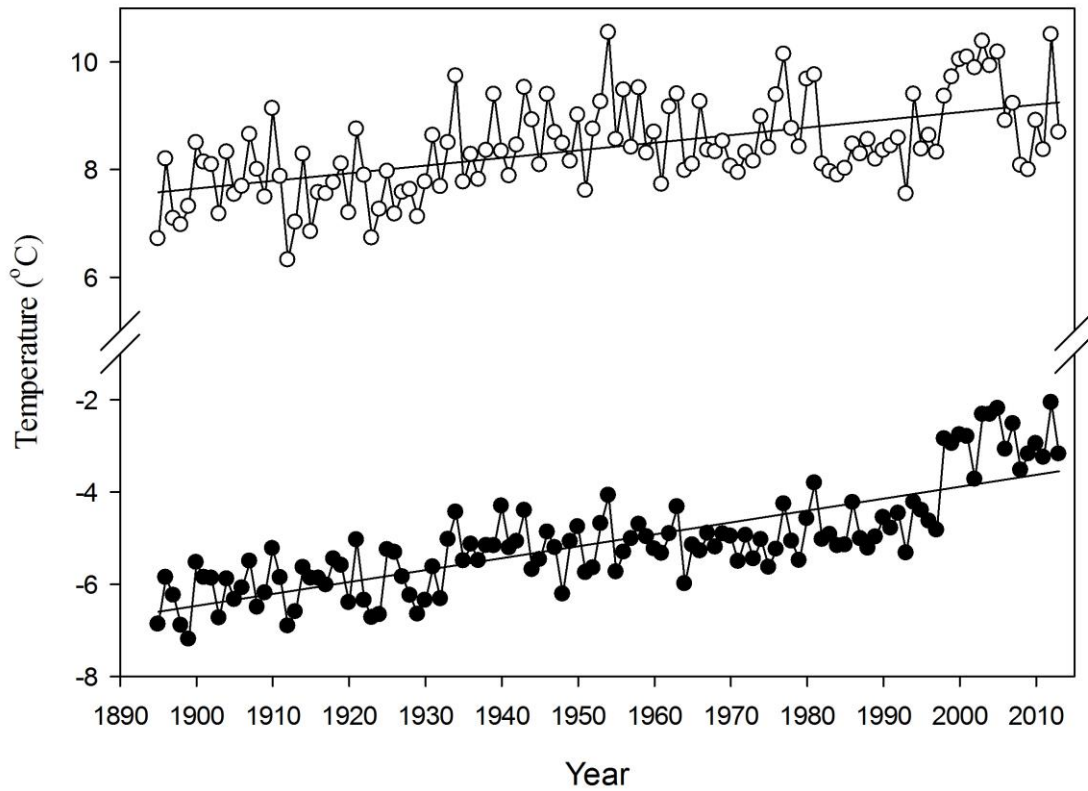


Figure 2: Mean annual minimum and maximum temperatures between 1895 and 2013 for Rocky Mountain National Park using 4K PRISM from four locations within RMNP.

Mean Annual Precipitation

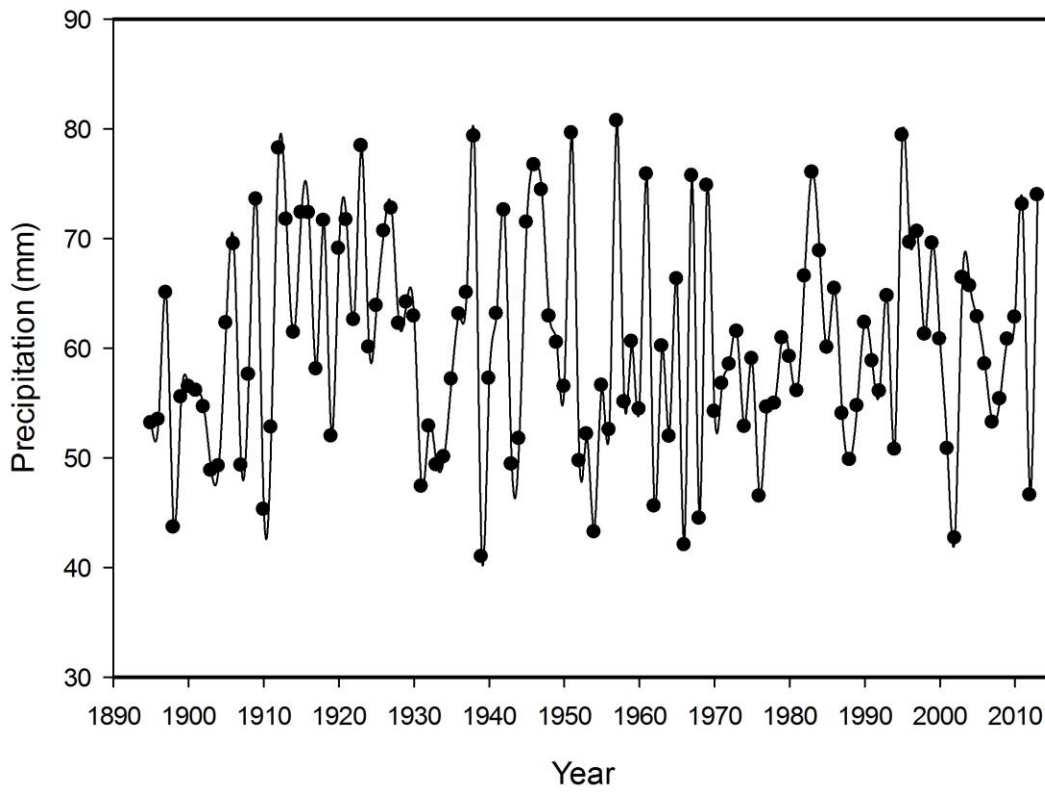


Figure 3: Mean annual precipitation between 1895 and 2013 for Rocky Mountain National Park. Data downloaded is 4K PRISM from four locations within RMNP.

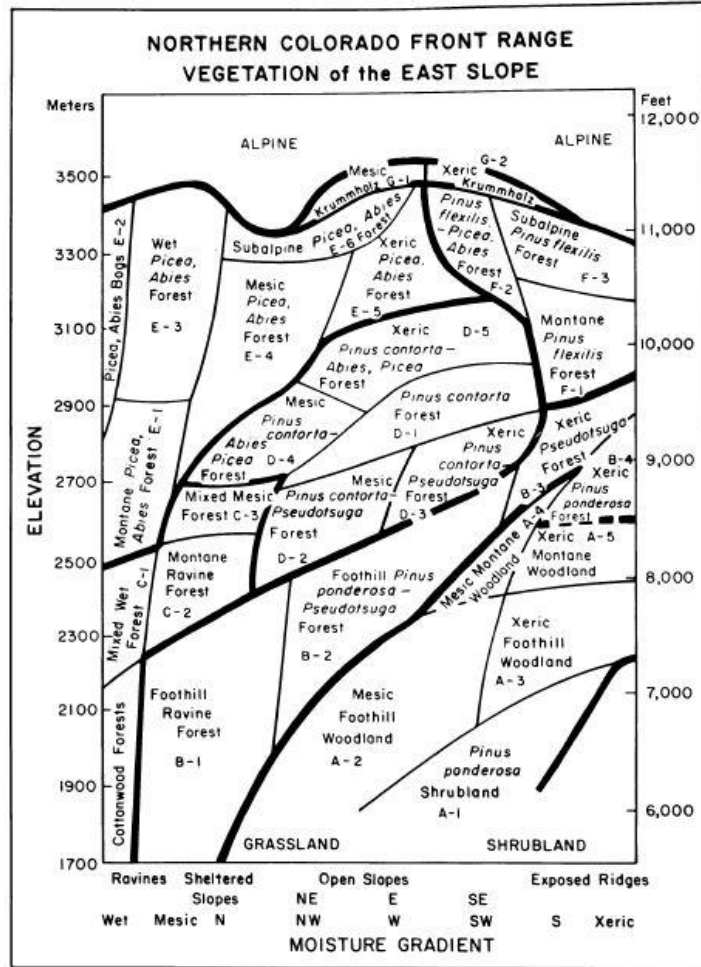


Figure 4: Community mosaic diagram showing the distribution of forests series relative to topographic and moisture gradients for the Colorado Front Range. Bold lines indicate series boundaries (from Peet 1981, with permission).

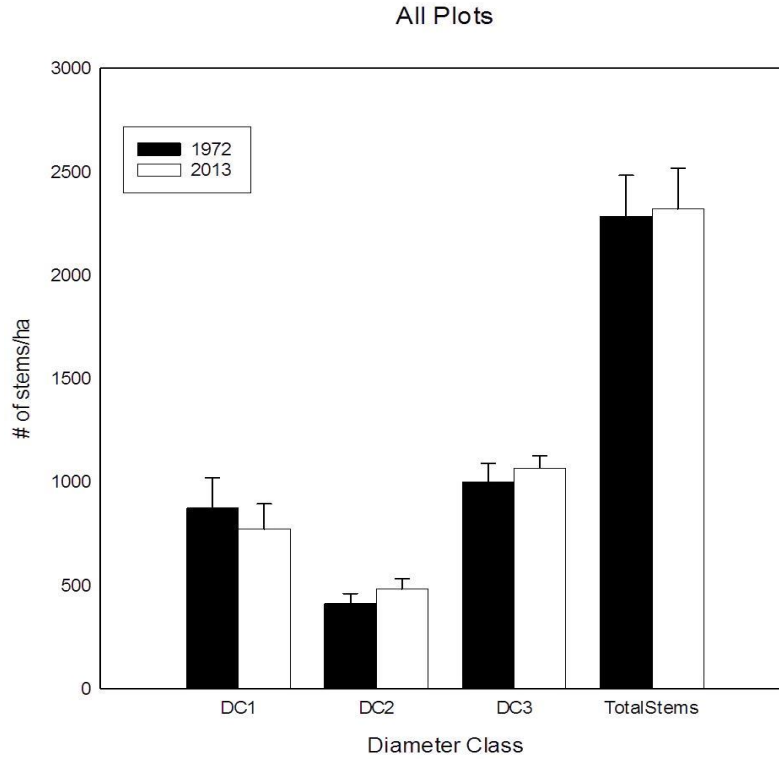


Figure 5: Mean number of stems per hectare plus SE for 1972 and 2013 for all species combined across all plots ($n = 63$) by diameter class. DC1 (0-2.54cm), DC2 (2.54cm-7.62cm) and DC3 (>7.62cm).

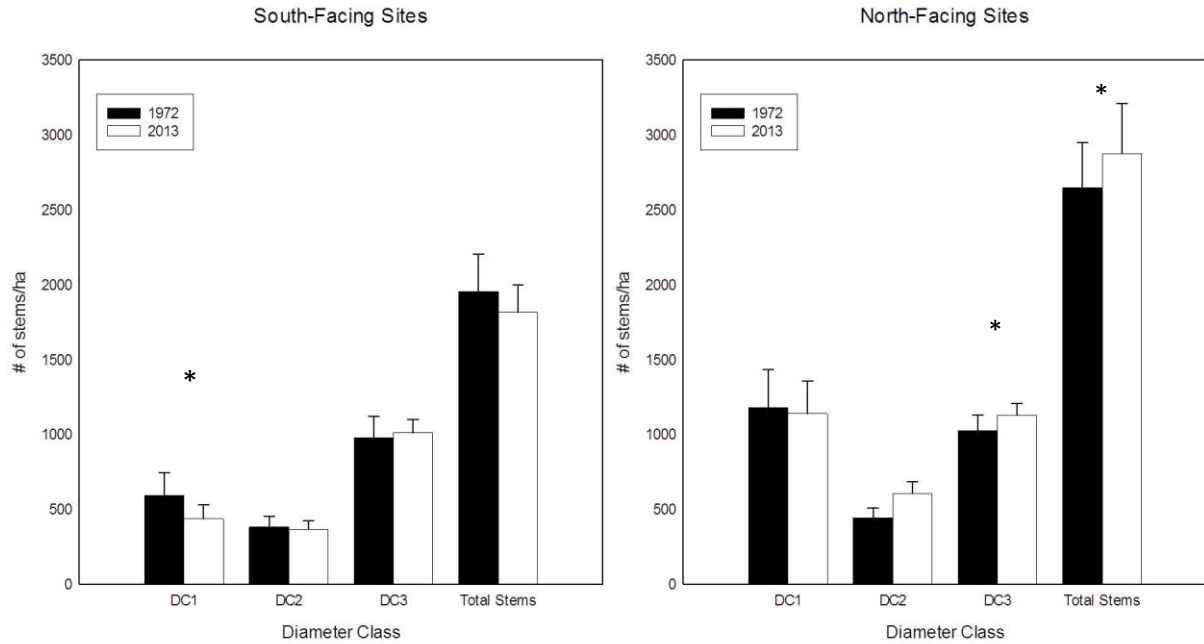


Figure 6: Mean number of stems per hectare plus SE for 1972 and 2013 for all species combined across south and north-facing aspects by diameter class. DC1 (0-2.54cm), DC2 (2.54cm-7.62cm) and DC3 (>7.62cm). Standard errors are for the means rather than the differences. Statistically significant differences between 1972 and 2013 indicated by * ($P < 0.05$) based upon Wilcoxon sign rank test.

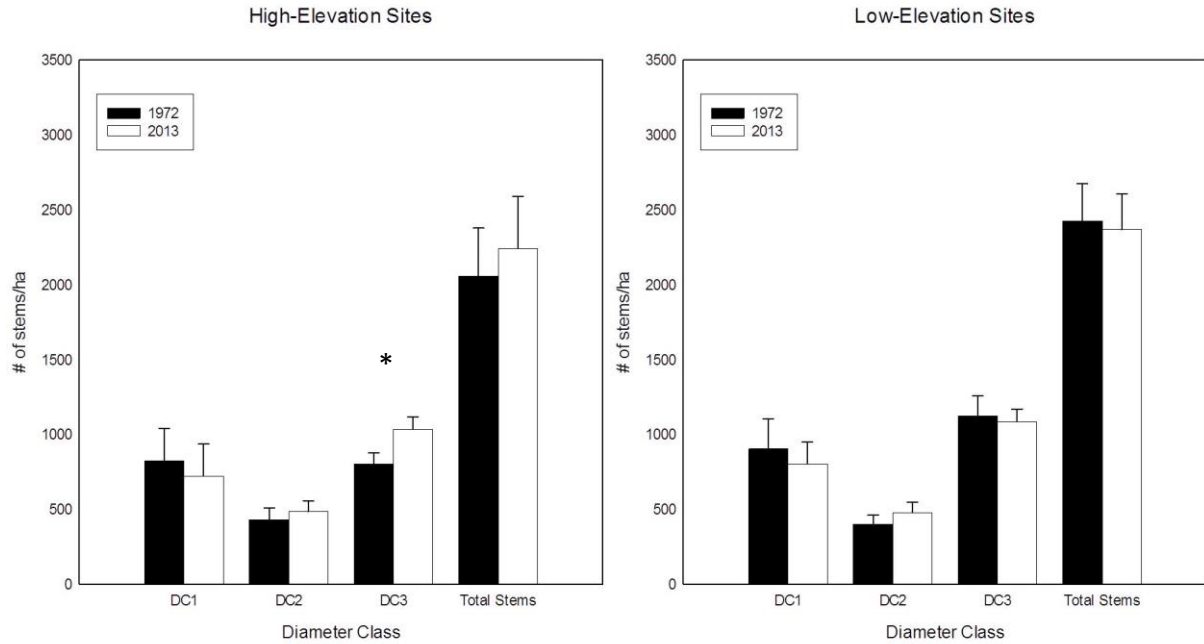


Figure 7: Mean number of stems per hectare plus SE for 1972 and 2013 for all species combined across high (>3048) and low-elevation sites (<3048) by diameter class. DC1 (0-2.54cm), DC2 (2.54cm-7.62cm) and DC3 (>7.62cm). Standard errors are for the means rather than the differences. Statistically significant differences 1972 and 2013 indicated by * ($P < 0.05$) based upon Wilcoxon sign rank test.

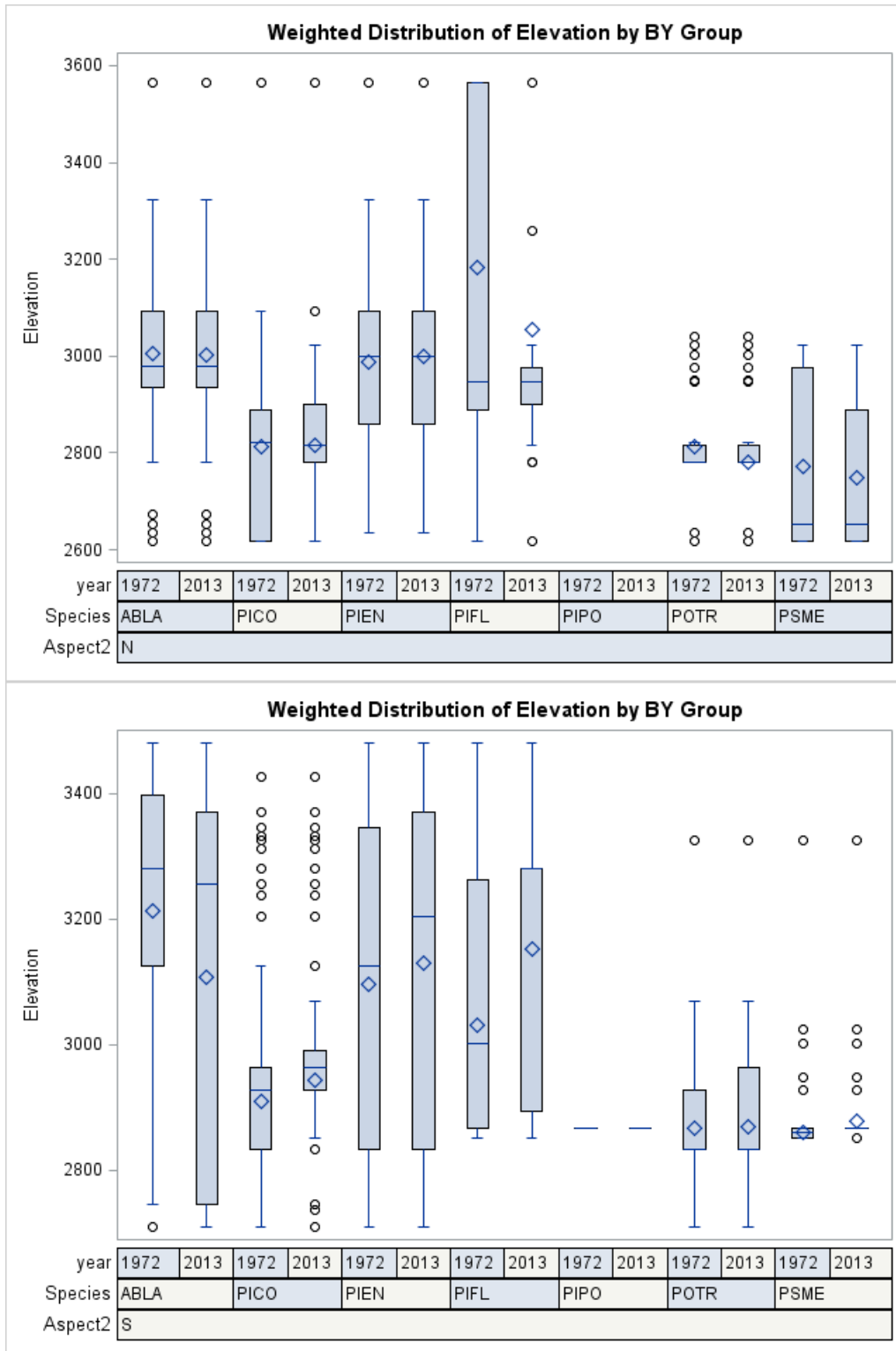


Figure 8: Differences between 1972 and 2013 datasets for mean (diamonds) and median (lines) elevation of DC1 (0-2.54cm) by species for both north-facing (top) and south-facing (bottom) slopes.

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