

Climate Change in the Rockies: Topographic Influence Over Vegetation Shifts

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ABSTRACT

Rising global temperatures have resulted in changes in plant phenology and range distributions, with the impacts being especially noticeable in mountain regions. In response to warming, vegetation often shifts to higher elevations, with treeline sometimes shifting upward tens of meters. To determine how trends in vegetation change in the Colorado Rocky Mountains relate to those observed at other mountainous sites throughout the world, I surveyed plant populations over nearly four decades at the Niwot Ridge Long-Term Ecological Research site using high-resolution aerial imagery. Overlaying land cover data from 1972 and 2008 for 2000 initial sample points onto a 10-meter Digital Surface Model (DSM) of the site, I conferred elevation, slope, and aspect variables to each point to determine how topographic factors limit or enhance vegetation shifts. While yearly temperatures at a weather station on site have shown a progressive decline in temperature since the early 1950's, Niwot Ridge has been warming during summer months over this same interval. This summer warming may contribute to vegetation shifts. Overall, tundra vegetation declined while shrubs and forests increased in cover. Tundra and shrub vegetation both experienced noticeable upward shifts in elevation, while forests seemed to infill with little upward expansion, possibly as a result of high wind speeds limiting establishment above treeline. Aspect and slope both had limited impacts on vegetation shifts, with forest expansion not being significantly affected by either factor.

KEYWORDS

climate change, vegetation shifts, tundra, shrub expansion, digital surface model

INTRODUCTION

Rising global temperatures have resulted in significant perturbations in global processes and continue to dramatically alter growing conditions for plant species (Walther 2003). The effects are amplified in mountain ecosystems, where plants are more susceptible to changes in temperature and other environmental factors (Smith et al. 2012). Over the past century alone, global temperatures have increased 0.6°C and are expected to rise between 1.4 and 5.8°C by the year 2100 (Beckage et al. 2008). Much of this recent warming has occurred within the past several decades; since 1976, the rate of warming was the highest for any period over the last 1,000 years (Beckage et al. 2008). As a result of warming, glacial extent has decreased significantly in arctic and alpine ecosystems (Pockley 2001, Zwiers 2002). The rising temperatures and shifts in glacial extent have varying effects on plants in herbaceous alpine communities and sub-alpine forests.

Climate has two primary impacts on plant species (Parmesan and Yohe 2003, Lenoir et al. 2008). The first involves shifts in plant phenology, or the timing of biological cycles (Zhu et al. 2012). While other factors such as nitrogen deposition have also been shown to influence plant phenology in mountain ecosystems (Smith et al. 2012), warming plays the most significant role (Sparks and Menzel 2002). In general, spring conditions arrive 2.3 days earlier per decade, with temperature changes being most pronounced in winter and early spring (Sparks and Menzel 2002, Parmesan and Yohe 2003, Walther 2003). This effect, combined with later onsets of fall conditions, leads to a lengthening of the growing season (Keeling et al. 1996, Zhu et al. 2012). The phenologic impacts of climate change on plant communities are consistent over a wide array of locations and species (Sparks and Menzel 2002).

The second impact concerns geographic shifts of vegetation (Lenoir et al. 2008), though trends vary greatly between sites. As a result of changing thermal conditions in mountain ecosystems, plants have undergone shifts toward higher elevations (Pockley 2001, Parmesan and Yohe 2003, Peñuelas and Boada 2003). Researchers often dispute, however, as to the extent that this shifting occurs. Because atmospheric warming directly influences tree species' spatial growth patterns (Paulsen and Korner 2001), evidence that forests have migrated large distances along an upward altitudinal gradient has continually emerged (Peñuelas and Boada 2003, Beckage et al. 2008, Lenoir et al. 2008). However, factors such as high wind speeds, which often occur in the Rocky Mountains on west-facing slopes, can negate the warming effect and prevent shifting of the

tree line (Holtmeier and Broll 2010). Similar arguments arise when discussing herbaceous alpine species above the tree line. In some studies (Walther et al. 2005, Lenoir et al. 2008, Grabherr et al. 2009), alpine species were shown to dramatically shift upward in elevation, while others found that topographic factors such as the slope and aspect of a site play a greater role than atmospheric temperature in influencing shifting of low-growing vegetation (Bennie et al. 2006, Scherrer and Korner 2010). Some studies have even identified plants shifting to lower elevations as a result of climate-based changes in plant water balance (Crimmins et al. 2011). The current debate over altitudinal shifting patterns in mountain regions and the lack of large-scale analyses of such processes in the Colorado Rocky Mountains warrant quantification of such parameters.

In this study, I will investigate the extent to which plant communities at the Niwot Ridge Long-Term Ecological Research (LTER) Site in the Colorado Rocky Mountains have responded spatially to climate change over the past four decades. In particular, I will determine if there are differences between altitudinal shifting rates of alpine plant communities, shrubs, and sub-alpine forest species and how topography affects shifting rates for each vegetation type. I hypothesize that all vegetation types are shifting to higher elevations, and that steep slopes and southerly and west-facing aspects will impede vegetation shifts. The Niwot Ridge LTER is located in the Front Range of the Rocky Mountains, approximately 35 km west of Boulder, CO (niwot.colorado.edu). My study site within the boundaries of the LTER covers an altitudinal range from 3100 – 4100 meters from the subalpine forests of the Front Range up to the Continental Divide on the western boundary.

METHODS

Data collection methods

Climate data

To determine how temperature has varied at Niwot Ridge, I downloaded monthly average temperatures from the Niwot Ridge LTER website (niwot.colorado.edu), which spanned from 1953 to 2012. I then averaged monthly data for each year into seasons, seasonal transitions, and the full year. For the winter season, I averaged the months of December, January, and February

for each year. For spring, I averaged March, April, and May; for summer, June, July, and August; and for fall, I averaged September, October and November. For the seasonal transitions, I averaged December – May for winter – spring, March – August for spring – summer, June – November for spring – fall, and September – February for fall – winter. I also averaged all of the monthly values for each year to get yearly average temperatures.

Vegetation data

To document changes in vegetation over the past four decades at Niwot Ridge, I used high-resolution orthophotos to manually characterize ground cover and generate a transition matrix. One of the photos was a color-infrared image taken in 1972, and another was a true color photo taken in 2008 (Figure 1). Both photos have been topographically corrected and were available by download through the Niwot Ridge LTER website (niwot.colorado.edu). Since the 2008 photo was taken before summer, there was more snowpack and the alpine tundra vegetation was not nearly as visible as in the 1972 photo. I accommodated for this by also analyzing a 2012 true color, high-resolution photograph that is used as the World Imagery Basemap in ESRI ArcMap 10.2 (Environmental Science Research Institute) (Figure 1c). This photograph was in a different projection and could not be manipulated, so I visually overlaid it with the two orthophotos to account for image distortion and used it to approximate the 2008 tundra distribution.

I randomly generated 2000 sample points within a roughly 38 km² region of the site, which I selected to include the Green Lakes Valley, Niwot Ridge, and a range of topographic and vegetative features of the site. For each point, I recorded the ground cover in both 1972 and 2008. The cover class categories were: bare ground, permanent snowpack, rock, water, alpine tundra, shrub, open woodland, and closed canopy forest. I used the 2008 and 2012 images simultaneously to determine the land cover for 2008. This was useful particularly for discriminating between shrubs and alpine vegetation, which can look alike in aerial images. Since the alpine tundra vegetation was dormant in the 2008 photograph, I could quickly tell where shrubs were.

When classifying each point, I cycled through the 1972, 2008, and 2012 images several times. Because the spatial resolution was lowest in 1972, it was often difficult to determine the ground cover at some points without the aid of high resolution, true-color imagery. I established a system for classification that I used for each of the 2000 initial sample points. I started with the

1972 image, because vegetation shows up well as a result of plants reflecting strongly in the infrared portion of the electromagnetic spectrum. If the 1972 image showed a very slightly red, non-textured color, the ground cover was tundra vegetation. Shrubs appeared dark red or pinkish red and were patchy, roughly round, and slightly textured. Open woodland appeared similar to shrubs, but was darker red and had greater texture, mostly evident by irregular shadows cast upon the vegetation. In order to be considered open woodland, the point had to be touching tree vegetation that existed in patches or islands with less than 75% canopy cover within a 25-meter radius of the point. If the point landed on grassy vegetation within an open woodland, I classified the point as tundra vegetation. Closed canopy forests appeared very dark red, with highly textured, shadow-laden surfaces in the 1972 image.

For points that were submerged in water for either 1972 and 2008, I characterized the land cover as water for both years, since the lake levels would fluctuate year-to-year and provide false land cover changes. If the ground cover in 1972 was bright white, it was snow. Since the 1972 photo was taken during the late summer, all of the points indicating snow were either glaciers or semi-permanent snowfields, and remained snow cover in both the 2008 and 2012 photographs. If the surface was grayish, the cover could either be bare ground or bare rock. I used the 2008 image to discern between these two, since bare rock is not likely to change to bare ground over such a short timescale. Classification with the higher resolution, true-color 2008 image was much less involved than the 1972 image, as nearly all of the ground cover could be easily discerned.

I immediately discarded points classified as water and those that were indiscernible in either sampling year by heavy shadows cast by the terrain. I also removed points that I labeled as rock or snowpack, since these locations are highly unlikely to ever support vegetation and therefore should not be included in analyses. The remaining five categories, bare, tundra, shrub, open woodland, and closed canopy, comprised 1,576 final points for use in my analyses.

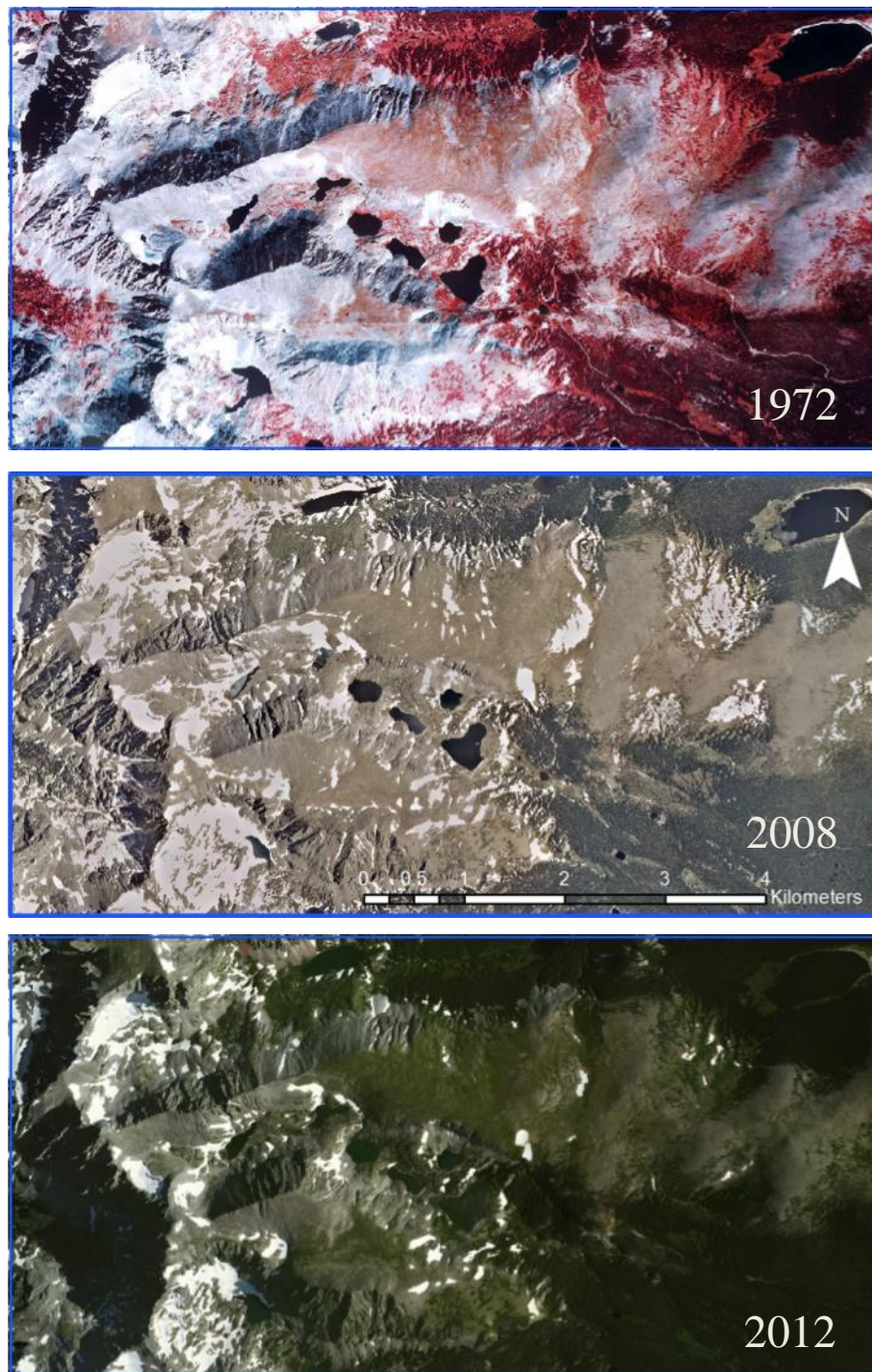


Figure 1. Sampling extent displayed in 1972 (top), 2008 (middle), and 2012 (bottom) imagery. The 1972 image is an infrared false-color image, causing vegetation to appear red. The 2008 and 2012 photos are both true color images, but the 2008 image appears much less green since it was taken earlier in the year before the growth of tundra vegetation.

Topographic factors

To generate topographic data, I used a 10-meter resolution digital surface model (DSM) (Manley et al. 2009) of the site to generate slope, elevation, and aspect variables (Figure 2). I measured slopes in degrees from zero to ninety and elevations in meters. I divided the aspects into eight compass directions: NW, N, NE, E, SE, S, SW, and W. Overlaying my 1,576 final classified sample points on the DEM in ArcMap 10.2, I conferred these three topographic variables to each data point. For each point, I then had the cover in 1972, cover in 2008, elevation (m), slope (degrees), and aspect.

Data analysis methods

Climate Data

After dividing the temperature data into yearly averages, seasons, and seasonal transitions, I ran logistic regressions in R Commander (Fox 2005) to determine the sign and significance of temperature trends.

Overall vegetation changes

From the 1,576 points, I generated a 5x5 vegetation change matrix, with each cell representing an individual transition for all of the possible combinations of 1972 and 2008 vegetation shifts. The cover categories in 1972 lined the vertical axis, while those for 2008 were along the horizontal axis. This matrix allowed for quick comparisons between relative abundances of each cover type in both years as well as the magnitudes of specific transitions and overall rates of percent change in cover for each vegetation type. To calculate the overall rates of change, I followed the methodology of Dial et al. (2007) (Equation 1).

$$100 * \ln(N_{2008}/N_{1972})/(3.6)$$

Eq. 1

This equation is a derivation of the exponential growth equation: $N=N_0e^{rt}$. In this case, $t = 3.6$, which is the number of decades between 1972 and 2008. The equation is multiplied by 100 to give the rate of change in terms of percent per decade.

Topographically controlled vegetation shifts

To determine how vegetation shifts were related to the topography of the site, I needed to determine both how vegetation was distributed along topographic gradients in 1972 and where along those gradients the greatest changes occurred for each vegetation type. I ran two general sets of logistic regression generalized linear models in R Commander (Fox 2005). In the first set, I modeled binary presence/absence data for each of the four vegetation types in 1972 in relation to the three topographic variables: slope, aspect, and elevation (Equation 2). I assigned absence of a given vegetation type at a given point a binary value of 0, and presence a binary value of 1. In the second set of logistic regressions, I used the same equation but selected different parameters for the binary variable. For these regressions, I modeled tundra decline as well as expansion of tundra, shrub, open woodland, and closed canopy forest. For tundra decline, I assigned a binary value of 0 (no change) for points that I identified as tundra in both 1972 and 2008, and assigned a value of 1 to points that were tundra in 1972 and changed to a different cover type by 2008, indicating decline. For each of the expansion transitions, I assigned a value of 0 to points that remained the same target vegetation type in both years, and a 1 to points that were something other than the target vegetation in 1972 that became the target vegetation by 2008. Here, the target vegetation refers to either tundra, shrub, open woodland, or closed canopy forest.

$$\text{Binary_variable} \sim \text{Elevation [Factor]} + \text{Slope [Factor]} + \text{Aspect [Factor]} \quad (\text{Eq. 2})$$

The generalized linear model shown in equation 2 was based on the binomial distribution and logit link function. Each of the input variables was categorical. I divided elevation into 10 x 100m intervals, slope into 7 x 10 degree intervals, and aspect into the eight compass directions discussed above.

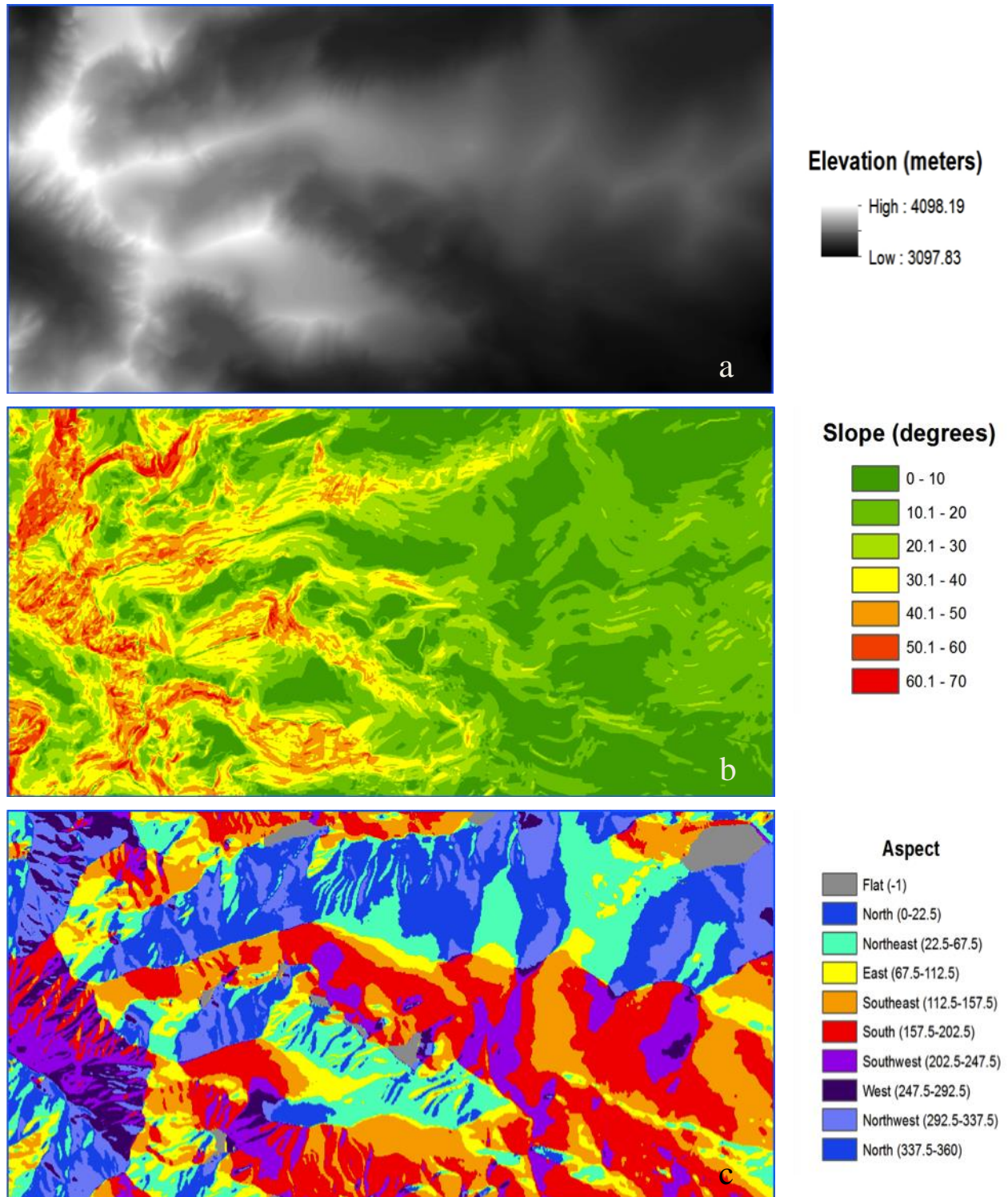


Figure 2. Digital Surface Model – derived maps of elevation (a), slope steepness (b), and aspect (c). The blue-outlined boundary of each map indicates the same sampling extent as shown above in Figure 1. The Continental Divide can be seen at the western edge of the boundary.

After running each logistic regression model, I exported the script into R (R Core Team 2013) for further analyses. I conducted ANOVAs on each of the generalized linear models in the “car” (“Companion to Applied Regression”) package (Fox and Weisberg 2011). For each presence/absence or vegetation shift model, the ANOVA analysis indicated which of the three topographic variables contributed significantly to the model, and which didn’t.

Once I determined which topographic variables were significant for each of the 8 generalized linear models, I ran single-step pairwise Tukey comparisons using the “multcomp” (“Multiple Comparisons Using R”) package (Hothorn et al. 2008) for each significant topographic factor. To do this, I created separate generalized linear models for each significant topographic factor, if any, from each of the original 8 models. Each of these new models had only had two variables: the topographic explanatory variable and the binary response variable, which could either be presence/absence or change/no change as discussed above. The pairwise comparisons of the categorical data allowed for quick comparisons of vegetation change along elevation, slope, and aspect gradients.

RESULTS

Climate Data

Temperature changes over the past 60 years at Niwot Ridge were complex, and for the most part, indicated cooling (Table 1), agreeing with previous research (Pepin and Losleben 2002). Of the nine temporal periods that I tested, only summer, winter, and fall – winter periods had significant relationships. Summer temperatures increased significantly ($p = 0.0073$) while there were significant negative trends in winter ($p = 0.0054$) (Figure 3) and fall – winter temperatures ($p = 0.0051$). There was a nearly statistically significant trend of decreasing fall temperatures as well ($p = 0.055$) (Table 1).

Table 1. Results of climate regressions. P-values marked with the * symbol are statistically significant. These significant trends are: increasing summer temperatures and decreasing winter temperatures, as well as decreasing fall – winter transition temperatures. Decreasing fall temperatures approached significance.

	Temporal Period	Months Averaged	t - value	P - value
	Year	1 - 12	-0.911	0.366
Seasons	Spring	3, 4, 5	0.11	0.913
	Summer	6, 7, 8	2.782	0.0073 *
	Fall	9, 10, 11	-1.962	0.055
	Winter	12, 1, 2	-2.893	0.0054 *
Transitions	Winter - Spring	12, 1 - 5	-1.585	0.118
	Spring - Summer	3 - 8	1.476	0.145
	Summer - Fall	6 - 11	0.095	0.925
	Fall - Winter	9 - 12, 1 - 2	-2.912	0.0051 *

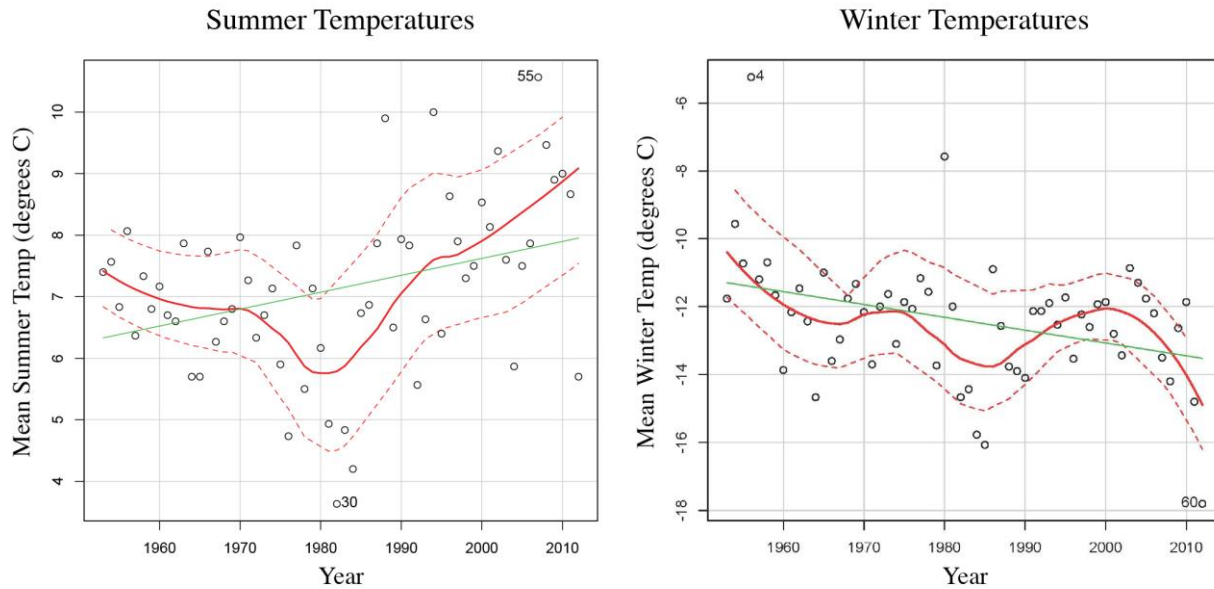


Figure 3. Comparison of summer and winter temperature trends between 1953 and 2012 at Niwot Ridge. The fall – winter transition was also significant, but the graph was similar to that for winter temperatures and is not shown.

Overall Vegetation Changes

Between 1972 and 2008, there was a slight trend toward increasing cover of woody vegetation across the site. I analyzed five land cover classes (in order of increasing woodiness):

bare ground, alpine tundra, shrub, open forest, and closed canopy. For the most part, land cover remained unchanged over the sampling period; however, encroachment by woody vegetation into areas previously characterized by other cover is an observable trend in the data (Table 2). The cover of bare ground decreased nearly 5% per decade, while alpine tundra vegetation decreased by 0.5% per decade. The other three cover types increased across the site. For tree cover, closed canopy forest cover increased by a mere 0.6% per decade and open woodlands increased by nearly 4% per decade. The largest increase in cover was from shrub expansion, which accounted for a nearly 8% per decade increase (Table 2).

Table 2. Land cover change matrix for the years 1972 and 2008. Each number represents the number of sample points, out of 1576, within each category. The rate of change was calculated as: $[100 * \ln(N_{2008}/N_{1972}) / (3.6)]$, where 3.6 represents the number of decades between 1972 and 2008 (Dial et al. 2007).

Land Cover Classification		2008					Total (1972)
		Bare	Tundra	Shrub	Open Forest	Closed Canopy	
1972	Bare	291	39	13	4	0	347
	Tundra	0	578	27	26	1	632
	Shrub	0	0	91	8	0	99
	Open Forest	0	3	0	182	6	191
	Closed Canopy	0	0	0	0	307	307
Total (2008)		291	620	131	220	314	1576
Rate of change (% per decade)		-4.9	-0.5	+7.8	+3.9	+0.6	

The diagonal line of cells extending from the upper left-hand corner to the lower right indicates static cover transitions. Above this line, there is an increase in woodiness, and below, a decrease. There were only several instances where there was a net decrease in woodiness; at three sample points, the cover changed from open woodland to alpine tundra. Shifts to increased woodiness were much more common. There were transitions from bare ground to tundra, shrub, and open woodland; tundra to shrub, open woodland, and closed canopy; shrub to open forest; and open forest to closed canopy (Figure 4).

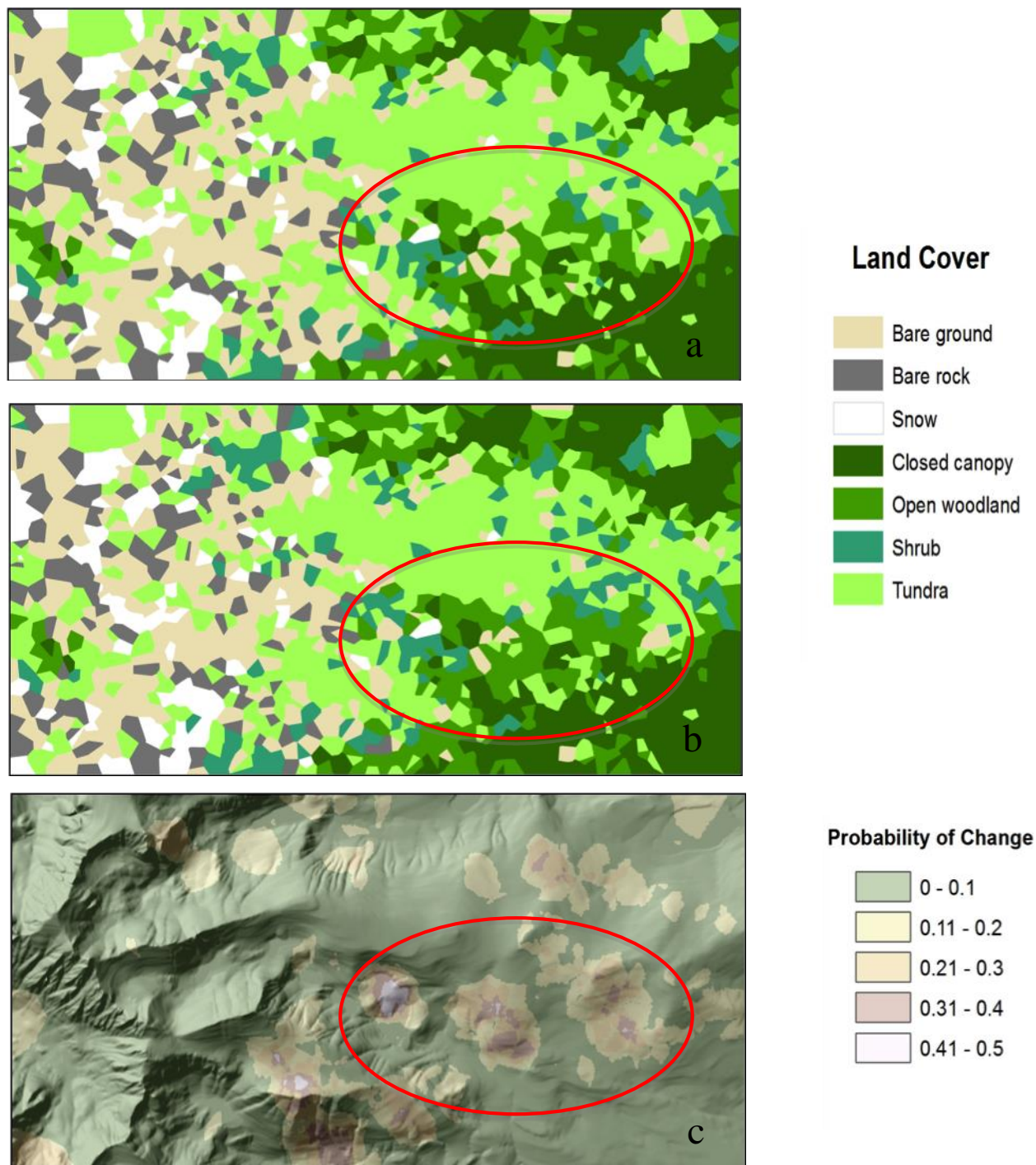


Figure 4. Land cover change. The top two images display the land cover classification, shown with thiesen polygons, for 1972 (a) and 2008 (b). Bare ground, bare rock, and snow are only incorporated for visualization and were not included in analyses. The bottom image (c) depicts hotspots of vegetation changes with warmer colors indicating greater change, and was made by kriging binary change/no change data for each point. The red outline indicates a region of relatively high probabilities of change.

Topographic factors

1972 vegetation distributions

Not all of the topographic variables were significantly correlated with the presence or absence of the different vegetation types in 1972. Elevation was significantly related to the presence of all vegetation types, while slope was related to all vegetation types except shrubs. Aspect did not play a role in any of the types except for closed canopy forests (Figure 5).

Tundra vegetation peaked at intermediate to high elevations, particularly in the 3400 – 3700 meter range and was present across the entire altitudinal range. It was less likely to be found at both lower and higher elevations, especially from 3100 – 3300 meters and 3900 – 4000 meters (Figure 5a). A large majority of the sample points in both years were tundra vegetation, so the percent cover of altitudinal bands that are not at the peak of the distribution is still relatively high. In terms of slope, tundra vegetation was roughly evenly distributed along slopes from 0 – 60 degrees. The only significant difference occurred between 10 – 20 degree slopes and 30 – 40 degree slopes, with higher tundra presence on the 10 – 20 degree slopes (Figure 5e). Aspect was insignificant in determining tundra distribution.

Shrubs peaked at lower elevations than tundra vegetation, predominantly in the 3300 – 3500 meter range, and extended from 3100 – 3700 meters in elevation (Figure 5d). There were no shrubs sampled in the 3700 – 4000 meter range. Because shrubs were overall the most rare vegetation type in the sampling extent (Table 2), the percent cover of shrubs in each altitudinal band does not exceed 20 percent of the band area. Unlike tundra vegetation, slope steepness was not significantly correlated with shrub presence in 1972; aspect was also insignificant.

Both elevation and slope steepness were significantly correlated with open woodland presence in 1972. This vegetation type spanned from 3100 – 3500 meters in elevation, peaking between 3200 and 3400 meters and having lower percent cover from 3100 – 3200 meters and 3400 – 3500 meters (Figure 5b). Open woodland was most prominent along slopes from 0 – 30 degrees, with significantly lower cover on 30 – 40 degree slopes than on 20 – 30 degree ones (Figure 5f). Aspect did not contribute significantly to open woodland presence in 1972.

All three topographic variables did, however, significantly correlate with closed canopy forest presence. Closed canopy forests decreased rapidly with elevation, covering over 80% of the

3100 – 3200 meter areas of the site and almost 0% of the 3400 – 3500 meter range. There were no points categorized as closed canopy forest above 3500 meters in elevation (Figure 5c). A similar trend occurred with slope steepness. Closed canopy forests progressively declined from a maximum coverage on 0 – 10 degree slopes to nearly 0% cover on 30 – 40 degree slopes, with 0% cover above 40 degrees (Figure 5g). There were not as clear of trends for aspect. Closed canopy forests were significantly more likely to be found on NW and S-facing slopes compared to N and NE slopes (Figure 5h).

Vegetation shifts

Elevation was significantly correlated with four of the vegetation transitions: tundra decline, tundra expansion, shrub expansion, and open woodland expansion. Slope steepness and aspect were not significantly related to any transition. Closed canopy forests did not expand significantly with respect to any of the topographic variables, including elevation.

Tundra expanded at both ends of its 1972 distribution, with equal probabilities of expansion for the 3200 – 3400 meter and 3600 – 4000 meter ranges (Figure 6a,e). However, tundra had an even greater probability of declining at lower elevations than expanding, particularly in the 3100 – 3500 meter range (Figure 6a,d). Both shrub (Figure 6b,f) and open woodland vegetation (Figure 6c,g) expanded equally over their entire elevation ranges, with no significant peaks in expansion on an altitudinal gradient. On the other hand, closed canopy forests did not expand at all, given that closed canopy forests only experienced about a 2% increase over the entire sample period (Table 2).

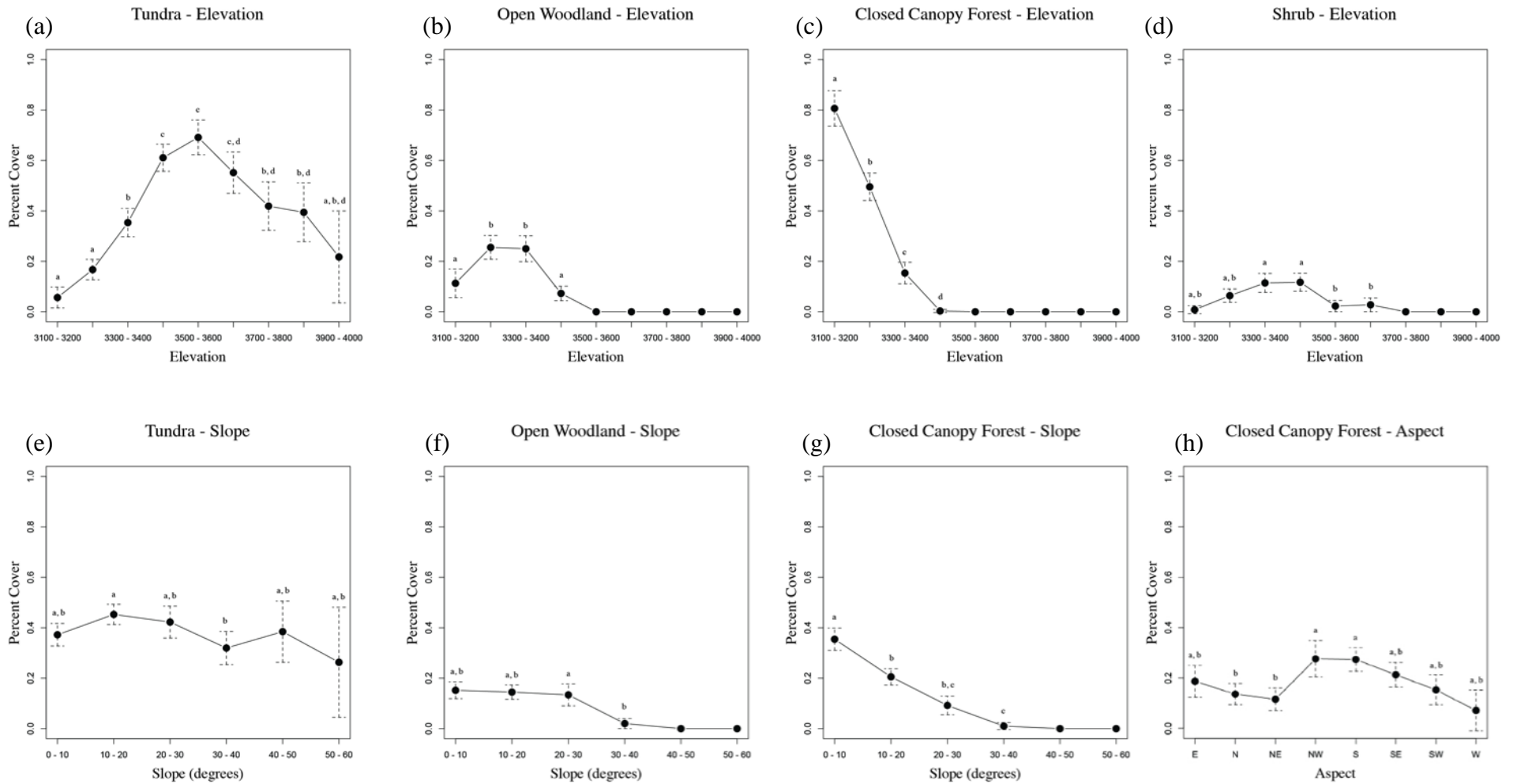


Figure 5. Topographic factors significantly correlated with vegetation presence in the 1972 image. Tundra presence was influenced by slope elevation (a) and slope (e); open woodland was also affected by elevation (b) and slope (f). Shrub presence was only correlated with elevation (d), while closed canopy forest presence was correlated with elevation (c), slope (g), and aspect (h). The vertical axis corresponds to the percent cover of each categorical bin on the horizontal x-axis.

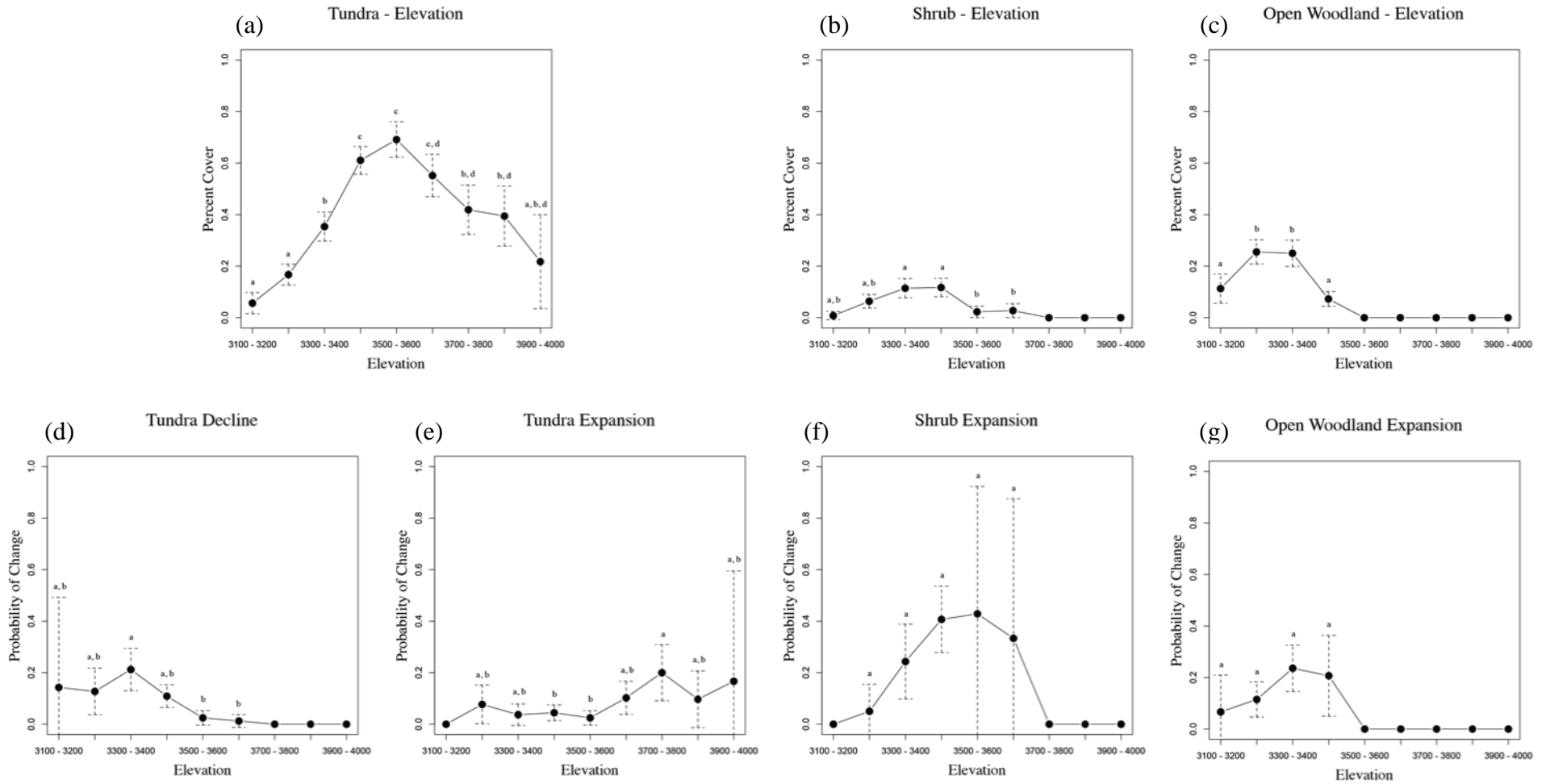


Figure 6. Vegetation transitions along an elevation gradient compared with 1972 altitudinal distributions. The vertical axis for each of the vegetation transitions (d – g) gives the probability of that transition of occurring within the corresponding elevation bin on the horizontal axis. The 1972 distributions with respect to elevation for tundra (a), shrub (b), and open woodland (c), are shown for comparisons. There were no significant shifting trends for closed canopy forests.

DISCUSSION

Despite overall cooling trends since 1953 at the Niwot Ridge LTER site (Pepin and Losleben 2000), summer temperatures are actually increasing at the site (Table 1, Figure 3) and overall temperatures have been increasing over the past two decades (Mitton and Ferrenberg 2012). Consequently, some of the vegetation changes, particularly shrub encroachment and alpine tundra decline, are consistent with those observed at warming arctic and alpine tundra sites (Hobbie and Chapin 1998, Dial et al. 2007). However, other changes characteristic of warming regions, notably dramatic upward tree line shifting (Peñuelas and Boada 2003, Beckage et al. 2008), do not appear to be occurring at Niwot Ridge. This suggests that, while warming plays a role, other factors are actively involved in regulating vegetation change. Grazing by elk (Schoenecker et al. 2004), increased nitrogen deposition from anthropogenic sources (Theodose and Bowman 1997, Madan 2007), and high wind speeds (Holtmeier and Broll 2010) may all influence vegetation shifts in positive or negative ways.

Changes in alpine tundra vegetation

The decline of alpine tundra vegetation at lower elevations suggests that it is becoming out-competed by woody vegetation in warmer regions of the site. Since air temperatures decrease by approximately 6 degrees Celsius per 100 meters in vertical elevation (Beckage et al. 2008), tundra vegetation growing at lower elevations may be stressed by increasingly arid conditions. The regions of maximum tundra decline are those from 3100 – 3500 meters, coinciding directly with expansion of shrubs and open woodland (Figure 6).

While tundra slightly declined overall and at low elevations, it expanded at high elevations. The peak in tundra expansion occurred along an altitudinal range that still had relatively high tundra abundance, but was on the upward edge of the 1972 distribution (Figure 6a). This indicates that tundra is shifting to higher elevations. Considering this effect and the net decline at lower elevations, the entire tundra distribution is shifting uphill. Because alpine tundra vegetation has nearly reached the highest elevations of the site, net decreases in cover in the coming decades may become larger, as the vegetation has increasingly less space to shift to. Additionally, if warming

trends intensify, as they are expected to globally (Torn and Harte 2006), the loss of tundra vegetation could be even more dramatic.

Shrub Dynamics

Shrubs expanded most rapidly on the site, suggesting similarity between Niwot Ridge and other warming sites. Shrub expansion is typically the greatest signal of climate warming and ecosystem change in mountain regions (Hobbie and Chapin 1998, Stow et al. 2004), and with a shrub population growth rate of nearly 8% per decade, Niwot Ridge clearly shows this trend. Shrubs significantly expanded across their entire distribution, including in the 3500 – 3700 meter range, which had minimal shrub cover in 1972 (Figure 6b). This suggests that, as opposed to tundra which experienced its full distribution shifting upwards, shrubs extended their ranges uphill. Shrub expansion, while affected by air temperatures, also can result from altered disturbance regimes, changes in grazing, fires, and anthropogenic activities (Meyers-Smith et al. 2011). For example, elk grazing, a prominent feature of Niwot Ridge, can reduce shrub growth by up to 98% (Schoenecker et al. 2004), counteracting climate-driven shrub expansion. So there may be factors other than temperature and topography that promote or inhibit shrub expansion.

Forest Dynamics

Closed canopy forests do not mirror trends observed in warming regions throughout the world. In some mountain region tree line studies, tree line shifted upwards in elevation by tens of meters (Peñuelas and Boada 2003, Beckage et al. 2008), while at Niwot Ridge, there was no significant increase in closed canopy cover. Open woodland, on the other hand, expanded significantly across its entire distribution, including in the 3400 – 3500 meter range. In 1972, this altitudinal range had minimal open woodland cover (Figure 6c), suggesting that, like shrubs, open woodlands are expanding their distributions uphill as opposed to experiencing upward shifts in their whole distribution. This suggests that trees are shifting to higher elevations in a patchy, as opposed to uniform, movement pattern. Even if temperatures were to increase at the site, however, it is unlikely that dramatic upward shifts would occur in the tree line, since strong westerly winds strongly regulate the establishment and growth of trees at Niwot Ridge (Holtmeier and Broll 2010).

Slope and aspect

There may be several factors for slope and aspect not contributing significantly to vegetation shifts. First of all, slope is slightly auto-correlated with elevation; the steepest slopes tend to occur at the highest elevations and the gentlest slopes occur at the lowest elevations (Figure 2). It could be, then, that adding slope to a generalized linear model that already accounts for elevation does not significantly improve the fit of the model. On the other hand, no vegetation occurred on the steepest slopes, so the model had no variability over certain slope ranges. This could limit the power of the model to discriminate between slope classes. In terms of aspect, it would make sense that different plants would expand differentially on slopes facing different directions due primarily to radiation loading, particularly on southwest facing slopes (Haase 1970, Bennie et al. 2008). It may be that, since I chose to analyze broad vegetation types, my analysis averages over differential sensitivities to drought stress and other effects of aspect. For example, there are 6 distinct tundra community types (niwot.colorado.edu), ranging from dry to mesic, that would probably be affected by aspect. However, I labeled all of these community types as a single tundra vegetation class, hence eliminating this variability.

Overall findings

Summer warming may play a significant role in regulating vegetation shifts at Niwot Ridge, but other factors can actively counteract vegetation shifts. Elk grazing can dramatically limit shrub growth (Schoenecker et al. 2004), and heavy winds can limit tree establishment (Holtmeier and Broll 2010). Despite grazing pressure, shrubs have expanded significantly. On the other hand, open woodland and closed canopy forests have expanded only slightly, suggesting that inhibitory factors such as wind speed nearly equal the summer growth season warming effect. Overall, only elevation significantly affected vegetation shifts, resulting in tundra shifting to higher elevations, as well as shrubs and open woodland slightly expanding their ranges uphill. Closed canopy forests did not show any significant signs of increasing in cover throughout the sample region.

Limitations and Future Directions

The limited availability of high-resolution historical orthophotos of the site was the main challenge posed by this study. The 1972 color infrared aerial photo was the earliest non-black-and-white aerial photograph that I could find on the Niwot Ridge LTER site. While it had high resolution, and infrared bands make vegetation easy to detect, it sometimes made it difficult to distinguish vegetation types from one another. For example, young shrub seedlings and tree seedlings may look identical to tundra vegetation, so the rate of woody expansion could be slightly over-expressed. Additionally, wet tundra meadows had a similar signature to shrubs, so it was difficult to identify vegetation shifts in these regions.

With the increasing availability of high resolution aerial and satellite imagery, these problems will not persist to the same degree in the coming decades. Remote sensing technology is constantly improving, and computer algorithms for classifying individual pixels are becoming more complex and robust. Future studies of vegetation change can take advantage of these improvements in technology to monitor Niwot Ridge over the next several decades and see if there are changes to the patterns that I have observed over the past 40 years. It is likely that, as climate change progresses, Niwot Ridge may begin to be influenced by changing thermal conditions, and more dramatic vegetation shifts could occur after some thresholds are passed.

Broader Implications

While, at present, the mechanisms behind some vegetation shifts remain mysterious, understanding the trajectories of the changes can aid in conservation and climate modeling interests. With a global decline in bees, for example, there may be interest in preserving existing alpine tundra habitat, which supports an impressive array of species that bees at elevation depend on. Other animals also make use of tundra vegetation, so it is vital to understand how tundra decline will affect these species. While elk consume large amounts of shrub biomass, they spend more time in mesic meadow vegetation (Schoenecker et al. 2004). The decline of tundra vegetation could therefore result in significant habitat losses for elk. Pikas, which gather forbs and other tundra vegetation in summer and store as food for the winter months (Wilkening 2011), could also be negatively affected by tundra decline. Conservation issues aside, these change trajectories also

have important climate feedback modeling implications. Changes in vegetation yield changes in albedo, carbon sequestration, and evapotranspirative fluxes, and hence provide important feedback mechanisms to climate change. Current climate models ignore these and various other climate feedbacks (Torn and Harte 2006), which could result in faster and more intense warming than we currently project. The information presented in this study could be used to both fill in the gaps in these climate feedback models and promote effective conservation planning in the Rockies.

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REFERENCES

Beckage, B., B. Osborne, D. G. Gavin, C. Pucko, T. Siccama, and T. Perkins. 2008. A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proceedings of the National Academy of Sciences* 105:4197-4202.

- Bennie, J., B. Huntley, A. Wiltshire, M. O. Hill, and R. Baxter. 2008. Slope, aspect and climate: spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecological Modelling* 216:47-59.
- Bennie, J., M. O. Hill, R. Baxter, and B. Huntley. 2006. Influence of slope and aspect on long-term vegetation change in British chalk grasslands. *Journal of Ecology* 94:355-368.
- Crimmins, S. M., S. Z. Dobrowski, J. A. Greenberg, J. T. Abatzoglou, and A. R. Mynsberge. 2011. Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science* 331:324-327.
- Dial, R. J., E. E. Berg, K. Timm, A. McMahon, and J. Geck. 2007. Changes in the alpine forest-tundra ecotone commensurate with recent warming in southcentral Alaska: Evidence from orthophotos and field plots. *Journal of Geophysical Research: Biogeosciences* (2005–2012) 112.
- Environmental Science Research Institute. 31 July 2013. ArcGIS ArcMap 10.2. Esri. Redlands, California, USA.
- Fox, J. and S. Weisberg. 2011. *An R Companion to Applied Regression, Second Edition*. Thousand Oaks, CA: Sage. < <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion> >
- Fox, J. (2005). The R Commander: A Basic Statistics Graphical User Interface to R. *Journal of Statistical Software*, 14(9): 1-42.
- Grabherr, G., M. Gottfried, and H. Pauli. 2009. Climate effects on mountain plants. *Nature* 369:448; 448.
- Haase, E. F. 1970. Environmental fluctuations on south-facing slopes in the Santa Catalina Mountains of Arizona. *Ecology* 51:959-974.
- Hobbie, S. E., and F. S. Chapin III. 1998. The response of tundra plant biomass, aboveground production, nitrogen, and CO₂ flux to experimental warming. *Ecology* 79:1526-1544.
- Holtmeier, F. and G. Broll. 2010. Wind as an ecological agent at treelines in North America, the Alps, and the European Subarctic. *Physical Geography* 31:203-233.
- Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous Inference in General Parametric Models. *Biometrical Journal* 50 (3), 346 – 363.
- Keeling, C. D., J. Chin, and T. Whorf. 1996. Increased activity of northern vegetation inferred from atmospheric CO₂ measurements. *Nature* 382:146-149.
- Lenoir, J., J. Gegout, P. Marquet, P. De Ruffray, and H. Brisse. 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320:1768-1771.

- Madan, N. J., L. J. Deacon, and C. H. Robinson. 2007. Greater nitrogen and/or phosphorus availability increase plant species' cover and diversity at a High Arctic polar semidesert. *Polar Biology* 30:559-570.
- Manley, W.F., Parrish, E.G., and Lestak, L.R., 2009, High-Resolution Orthorectified Imagery and Digital Elevation Models for Study of Environmental Change at Niwot Ridge and Green Lakes Valley, Colorado: Niwot Ridge LTER, INSTAAR, University of Colorado at Boulder, digital media.
- Mitton, J. B., and S. M. Ferrenberg. 2012. Mountain pine beetle develops an unprecedented summer generation in response to climate warming. *The American Naturalist* 179:E163-E171.
- Myers-Smith, I. H., B. C. Forbes, M. Wilmking, M. Hallinger, T. Lantz, D. Blok, K. D. Tape, M. Macias-Fauria, U. Sass-Klaassen, and E. Lévesque. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters* 6:045509.
- Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37-42.
- Paulsen, J. and C. Körner. 2001. GIS-analysis of tree-line elevation in the Swiss Alps suggests no exposure effect. *Journal of Vegetation Science* 12:817-824.
- Peñuelas, J. and M. Boada. 2003. A global change-induced biome shift in the Montseny mountains (NE Spain). *Global Change Biology* 9:131-140.
- Pepin, N., and M. Losleben. 2002. Climate change in the Colorado Rocky Mountains: free air versus surface temperature trends. *International Journal of Climatology* 22:311-329.
- Pockley, P. 2001. Climate change transforms island ecosystem. *Nature* 410:616-616.
- R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. < <http://www.R-project.org/> >
- Scherrer, D. and C. Koerner. 2010. Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Global Change Biology* 16:2602-2613.
- Schoenecker, K. A., F. J. Singer, L. C. Zeigenfuss, D. Binkley, and R. S. Menezes. 2004. Effects of elk herbivory on vegetation and nitrogen processes. *Journal of Wildlife Management* 68:837-849.
- Smith, J. G., W. Sconiers, M. J. Spasojevic, I. W. Ashton, and K. N. Suding. 2012. Phenological changes in alpine plants in response to increased snowpack, temperature, and nitrogen. *Arctic, Antarctic, and Alpine Research* 44:135-142.

- Sparks, T. H. and A. Menzel. 2002. Observed changes in seasons: an overview. *International Journal of Climatology* 22:1715-1725.
- Stow, D. A., A. Hope, D. McGuire, D. Verbyla, J. Gamon, F. Huemmrich, S. Houston, C. Racine, M. Sturm, and K. Tape. 2004. Remote sensing of vegetation and land-cover change in Arctic Tundra Ecosystems. *Remote Sensing of Environment* 89:281-308.
- Theodose, T. A., and W. D. Bowman. 1997. Nutrient availability, plant abundance, and species diversity in two alpine tundra communities. *Ecology* 78:1861-1872.
- Torn, M. S., and J. Harte. 2006. Missing feedbacks, asymmetric uncertainties, and the underestimation of future warming. *Geophysical Research Letters* 33.
- University of Colorado, Boulder. 12 July 2013. Niwot Ridge Long-Term Ecological Research Site. National Science Foundation. < www.niwot.colorado.edu >
- Walther, G. 2003. Plants in a warmer world. *Perspectives in Plant Ecology, Evolution and Systematics* 6:169-185.
- Walther, G., S. Beißner, and C. A. Burga. 2005. Trends in the upward shift of alpine plants. *Journal of Vegetation Science* 16:541-548.
- Wilkening, J. L., C. Ray, E. A. Beever, and P. F. Brussard. 2011. Modeling contemporary range retraction in Great Basin pikas (*Ochotona princeps*) using data on microclimate and microhabitat. *Quaternary International* 235:77-88.
- Zhu, W., H. Tian, X. Xu, Y. Pan, G. Chen, and W. Lin. 2012. Extension of the growing season due to delayed autumn over mid and high latitudes in North America during 1982–2006. *Global Ecology and Biogeography* 21:260-271.
- Zwiers, F. W. 2002. Climate change: The 20-year forecast. *Nature* 416:690-691.