

Talus Turnover: A Study of the Distribution of Lichens along Elevational Gradients

Student: Connor Bernard

Mentor: Quentin Read

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Abstract

Understanding the processes and mechanisms that underlie patterns of species diversity and distribution is a fundamental goal of community ecology. Elevational gradients enable ecologists to tease apart ecological drivers and mechanisms as reflected by distribution patterns. In spite of the considerable effort put forth in examining patterns of diversity along elevational gradients, relatively few studies have looked at lichen distributions along elevational gradients. In our study we aimed to address how lichen distributions vary with elevation. Lichen community surveys were conducted along two elevational gradients of granite talus spanning 600m in the Southern Rocky Mountains. Every 120m between 3170m and 3770m, lichen surveys were conducted for species occupancy, relative abundance, and lichen coverage in addition to covariates. Across all metrics weak correlation and low effect sizes indicated that elevation does not play a considerable role on community assemblage at this scale. This result encourages the consideration of alternative environmental factors driving differential assemblages in lichen communities which have played key roles in like studies.

Introduction

Understanding the processes and mechanisms that underlie patterns of species diversity and distribution is a fundamental goal of community ecology (Levin, 1992; Weins et al. 1993; Agrawal et al. 2007). Describing patterns in diversity is imperative to understanding ecological mechanisms and evaluating how systems might respond to disturbance. Elevational gradients enable ecologists to tease apart ecological drivers and mechanisms as reflected by distribution patterns (Lomolino, 2001; Körner, 2007; Nogues-Bravo, 2008). Elevational gradients act as an aggregate of various environment gradients, most notably moisture and temperature (McCain and Grytnes, 2010). For this reason, elevational gradients have been considered a proxy for climate gradients based on the assumption that moisture and temperature act as the principal components of climate. However, it is also recognized that additional environmental gradients may vary along elevation, such as solar radiation, air composition, and air pressure (Körner, 2007). Thus, elevational gradients may be viewed as broad environmental factors which include many covariates that drive differential community assemblages across their range. In recent years, elevational gradients have become the focus of a concerted effort in establishing biodiversity indices worldwide (McCain and Grytnes, 2010).

A variety of distribution patterns have been observed across taxa along elevational gradients. Among these richness patterns, four emerge with considerable frequency: decreasing, low plateau, low plateau with a mid-elevation peak, and mid-elevation peak. Meta-analyses have demonstrated linkages of these distribution patterns to specific taxa; for example, non-flying mammals display near ubiquitous mid-elevation peaks in diversity while bats consistently display either decreasing or mid-elevation peaks (Rahbek 2005; McCain and Grytnes 2010). In

spite of lacking meta-analyses, all four of these trends have been observed in the literature for groups of plants and insects as well. Analyses of diversity have been largely absent for microbes, however, with only one study documented (Byant et al., 2008; conducted along Washington Gulch outside of Gothic, CO) in which diversity declined with elevation. Though studies have extensively documented diversity along environmental gradients in plants (e.g. Kelly et al. 2008), animals (e.g. Moritz et al. 2008; Wilson et al. 2005), decomposition (e.g. Murphy et al. 1998), and phenology (e.g. Dunne et al. 2003), lichens – like microbes – have been largely neglected. Moreover, common pattern congruency across taxa might not be suspected to occur with lichens, insofar as the composite association of a fungus (>15,000 species) and algae (or cyanobacteria) (>30 species) produces a new trait assemblage defined by interactive effects often discrete from those displayed by either individual partner (Ahmadjian, 1967). Nonetheless, similarities with respect to the limited species which partake in the symbiosis could suggest similar trends among lichens as a composite group.

In spite of the comprehensive effort put forth in establishing diversity indices on elevational gradients, relatively few studies have looked at lichen distributions along elevational gradients (Holien, 1997; Bruun et al. 2006; Grytnes et al. 2006; Baniya et al. 2010; Kessler, 2000). Studies taking elevation into account have displayed differing distribution patterns in different locations (Bruun et al. 2006; Grytnes et al. 2006; Baniya et al. 2010), have demonstrated distribution limitations corresponding with epiphytic host distribution (Baniya et al. 2010), and have not controlled for habitat change along their gradients. Nonetheless, lichens lend themselves to this format of research in a variety of ways. Lichens inhabit nearly all environments and are a long lived species. In spite of their resilience to desiccation under drought conditions and their tolerance of temperature extremes, lichens are highly responsive

species with respect to light, nutritional availability, acidity, and air quality (Ahmadjian, 1967). Consequently, they can be used as a snapshot of environmental conditions at a specific point in time (Conti, 2001) while also reflecting long-term environmental conditions such as glacial recession and disturbance (Refsnider and Brugger, 2007). Understanding patterns in the diversity of lichens provides insight to those mechanisms underpinning their structure. Discerning these processes and drivers is essential to forecasting how lichens are likely to respond to disturbance; this is of considerable importance with respect to biological timekeeping, with respect to their utility as bio-monitors, and with respect to ultimate species survivorship in face of disturbance. The long-term temperature gradient on which we are evaluating lichen distribution may also be particularly relevant to the effects of climate change (Fukami & Wardle 2005).

To consider those mechanisms which might be exerting influence on the distribution of lichens, I investigated the relationship between elevation and lichen communities on White Rock Mountain east of Gothic, Colorado. For this study, I surveyed lichen species along an elevational gradient on a talus slope for richness, evenness, and abundance in addition to recording covariates related to microhabitat variation such as substrate, shading, and aspect. I hypothesized that richness would decline with elevation as exposure to extremes such as temperature, light intensity, and moisture surpasses the physiological limits of certain lichen species (as has been noted in other studies above tree line (e.g. Bruun et al., 2006). Furthermore, I hypothesized that evenness would decline with elevation as environmental stresses surpass species' tolerances with increased elevation, in effect, reducing competition for those species with higher tolerance and decreasing abundance of those with lesser tolerance. Last, I hypothesized that total abundance would decrease with elevation due to the physiological limitations of lichens which might be met at higher altitudes.

Methods

Site Selection

In order to determine sites for our elevational transects, I limited the total range of talus fields in the greater Gothic Valley region to those which (A) spanned both continuously and homogeneously (distance between rocks) at least 600 meters (m); (B) started higher than 3170 meters above sea level; and (C) extended beyond 3770 meters above sea level. This range was designed to maintain a gradient that transected tree line and to allow the possibility of broadening the study to comparable sites throughout the valley. Studies have found unimodal peaks in lichen diversity at treeline, attributable to the heterogeneity of habitat over the ecotone and greater light availability with dampened exposure to environmental factors of high altitude environments (Bruun et al., 2006). The nature of this stark habitat boundary represents a more radical example of the confounding influence of habitat change on lichen distribution. I therefore aimed to transect the same geographical and elevational range while controlling for this variable. Furthermore, I limited sites to those which maintained consistency in substrate along the length of the talus field. Talus fields which met these criteria but represented the most diversity by way of structure were located at two sites on White Rock Mountain: one on the northern aspect and the other on the western aspect. Along discrete elevation intervals (every 120m from 3170-3770m above sea level), a 5m x 5m site was established in the center of each talus field. Sites and elevation were located in the field using a handheld Garmin GPS unit. Within the 5m x 5m quadrat, twelve 20cm × 20cm plots were randomly assigned using R Statistical Software and measured out with a tape measure.

Species Counts

In each plot, species were analyzed visually and photographically documented. Species were keyed out using the *Consortium of North American Lichen Herbaria*, *A Rocky Mountain Lichen Primer* (Corbridge Jr., 1998), *A Color Guidebook to Rocky Mountain Lichens* (St. Clair, 1999), and *North American Lichens* (Brodo, 2001). Species occupancy and estimated relative abundance were then recorded. Estimates of lichen coverage, shading, and aspect were also made on site and confirmed photographically. Lichen response variables were then calculated for richness (total species per plot), total lichen abundance (estimate of cover area), evenness ($\lambda/\text{total species}$), Shannon-Wiener Diversity (H'), and Simpson Diversity (λ). Shannon-Wiener Diversity provides a metric for measuring the probability of predicting the next number in a given set as a function of those species in the set, or the uncertainty in a given series. Shannon-Wiener Diversity is consequently more sensitive to species richness within the set, though remains highly responsive to evenness. Simpson Diversity predicts the probability that two species, if chosen at random from a series, represent conspecifics. Simpson Diversity is therefore more responsive to evenness, while still somewhat sensitive to species richness. These two indices are therefore representative of the two potential biases in calculating diversity, favoring either richness or sensitivity, each of which has its advantages and disadvantages to management practices and predicting community responses to disturbance.

Statistical Analyses

The relationship between elevation and lichen response variables was analyzed using SAS JMP statistical software. Least square means at each elevation were calculated in addition to Analyses of Variance (ANOVA's), while R-Squared values and Probabilities of $F > 0$ were

calculated using linear regressions treating elevation as a continuous variable. To determine the best model for each response variable, various models (including quadratic and logistic) were evaluated with adjusted R-squared values.

Results

Richness (Fig 1), lichen cover (Fig 2), and evenness (Fig 3) all displayed statistically significant correlations with elevation ($p=0.0001$, 0.0001 , and 0.0039 respectively). Nonetheless, these linear correlations accounted for a rather marginal amount of the variability within the data ($R^2=0.116928$, 0.118216 , and 0.062871 respectively). The effect of these models, however, was considerably small ($f^2=0.132410$, 0.134065 , and 0.067089 respectively). Diversity indices further reflect this trend resultant to their constituent metrics (Shannon-Wiener (H') diversity (Fig 4) and Simpson (λ) diversity (Fig 5) $p= 0.0065$, 0.011 ; $r^2= 0.048609$, 0.041698 ; $f^2= 0.051092558$, 0.043512379 respectively).

Discussion

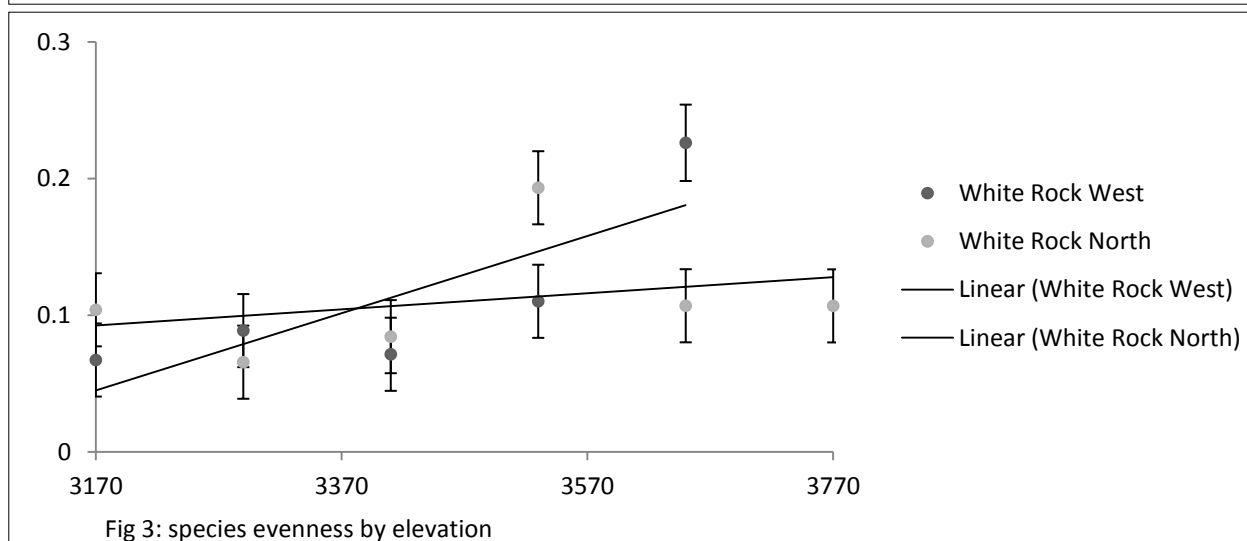
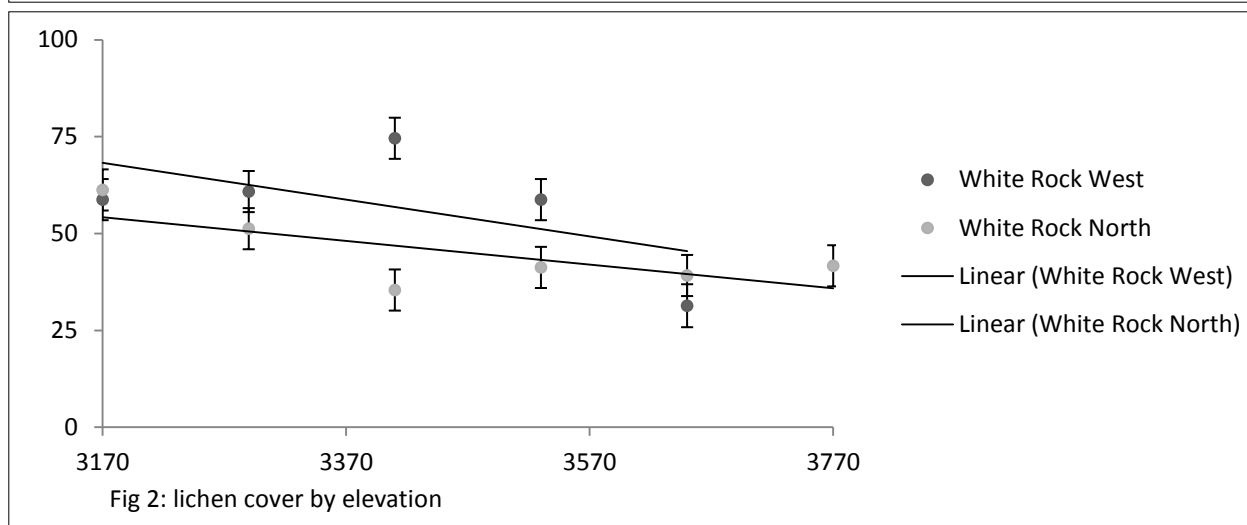
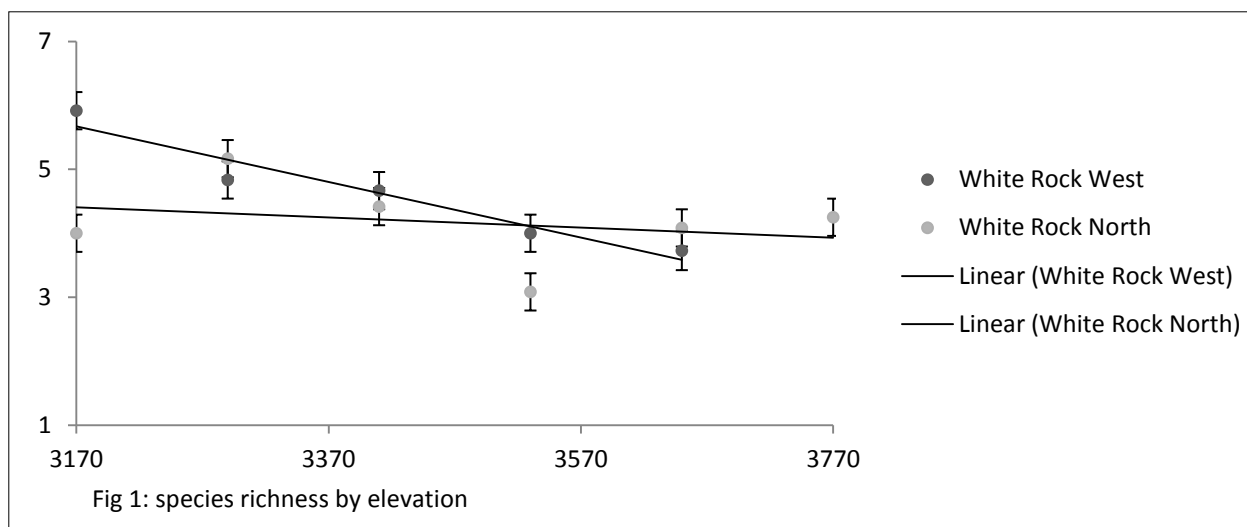
Elevation yielded significant correlation with richness, but accounted for a minimal amount of the variance in the data. Moreover, the effect of this correlation was considerably small. We can therefore conclude that the effect of elevation on lichen richness is of limited inference and rather marginal, especially in view of other factors which account for variability within the data. This trend was similarly iterated in both lichen cover (a proxy of lichen

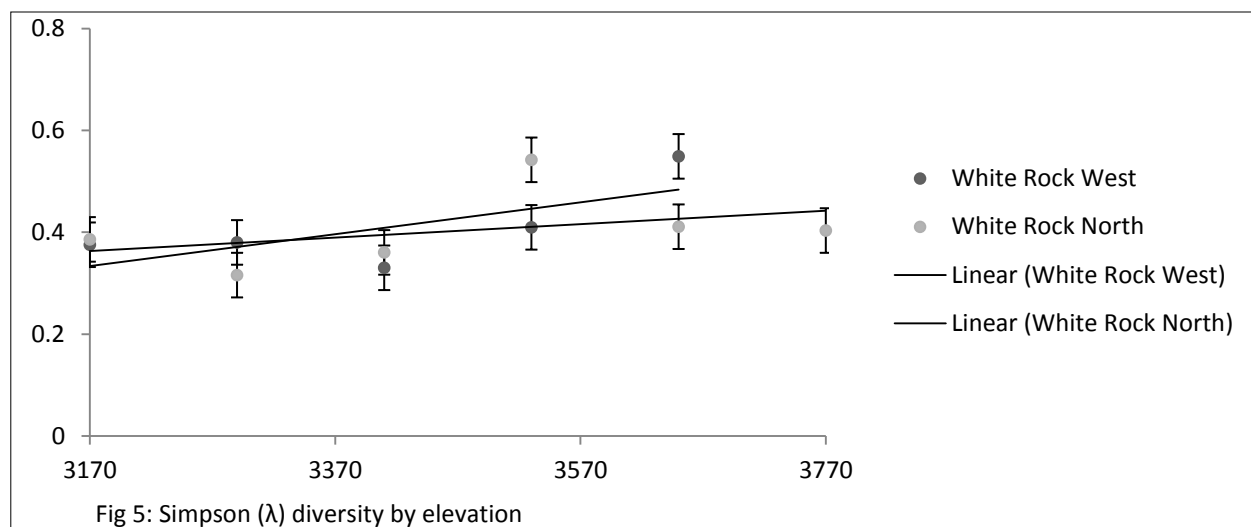
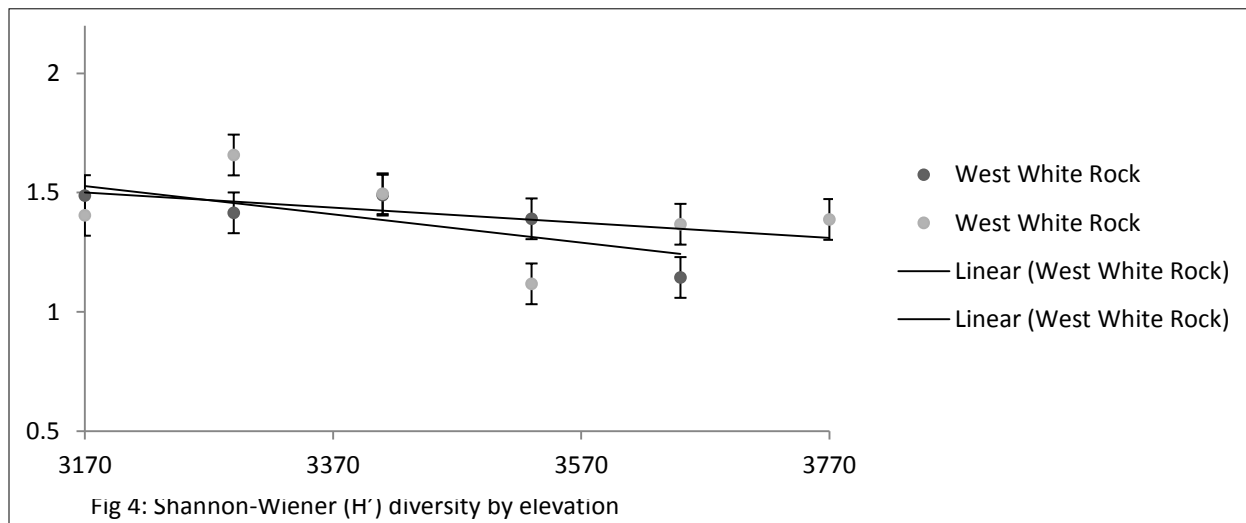
abundance) as well as evenness. Similar trends were reflected in diversity indices reflecting weighted calculations of its constituent variables (richness and evenness).

The consistent trend of weak correlation in both fit and effect demonstrates the marginal effect which elevationally correlated environmental gradients exert on lichen communities in this system. Similarly to how habitat change and tree line have largely defined distribution patterns along elevational gradients in the past (Kessler, 2000; Bruun et al., 2006; Baniya et al., 2010), distributional trends appear driven less by precipitation and moisture gradients (in addition to other environmental factors which change with elevation) and more by alternative variables which might be mediated to a greater extent by habitat variation. Environmental factors contingent to lichens such as pH, nutrient availability, and light intensity may be mediated to a greater degree by habitat type or disturbance than by elevation.

It is possible that variations among the sites studied were confounded in part by the effects of adjacent habitat or substrate. Habitat and substrate define parameters of soil composition, moisture regimes and hydrology, as well as a suite of other environmental characteristics comprehensive to light, temperature, and pH. Insofar as these environmental conditions are mediated and maintained by species composition, turnover in community structure as a consequence of substrate, climate, or other factors can have a severe consequence to both localized microhabitats as well as the ecosystem at large. Provided that these highly influential suites of environmental conditions foster particular lichen assemblages, their influence on the neighboring habitat could be significant, particularly with respect to dispersal limitations of lichens. Furthermore, those habitats which span into higher elevations could act as corridors and pathways to higher elevation talus which is otherwise less accessible to lichens due to exposure constraints. Another factor which could exert influence on community assemblage is lichen

distribution. To the extent that lichen dispersal is constrained to wind dispersal of spores or vegetative propagules (thallus structure fragmentation) (Ahmadjian, 1967), both the potential for lichen to colonize and their subsequent growth rates may be contingent on the proximity of conspecifics. Numerous studies have studied the limitations imposed by and implications of dispersal, including one study in which terricolous propagules managed to disperse just 68cm in the most favorable conditions (Hienken, 2006). Studies have not directly addressed the effects of prior lichen colonization on new colonization which could additionally exert influence on community composition. It is therefore in the interest of future studies to address the relative pressures exerted on lichen communities by these alternative gradients, and to understand how they might be expressed in different habitat types. Further study is also warranted to better understand how elevation mediates habitat structure and what scales are necessary for elevation to exert significant pressures on lichen distribution.





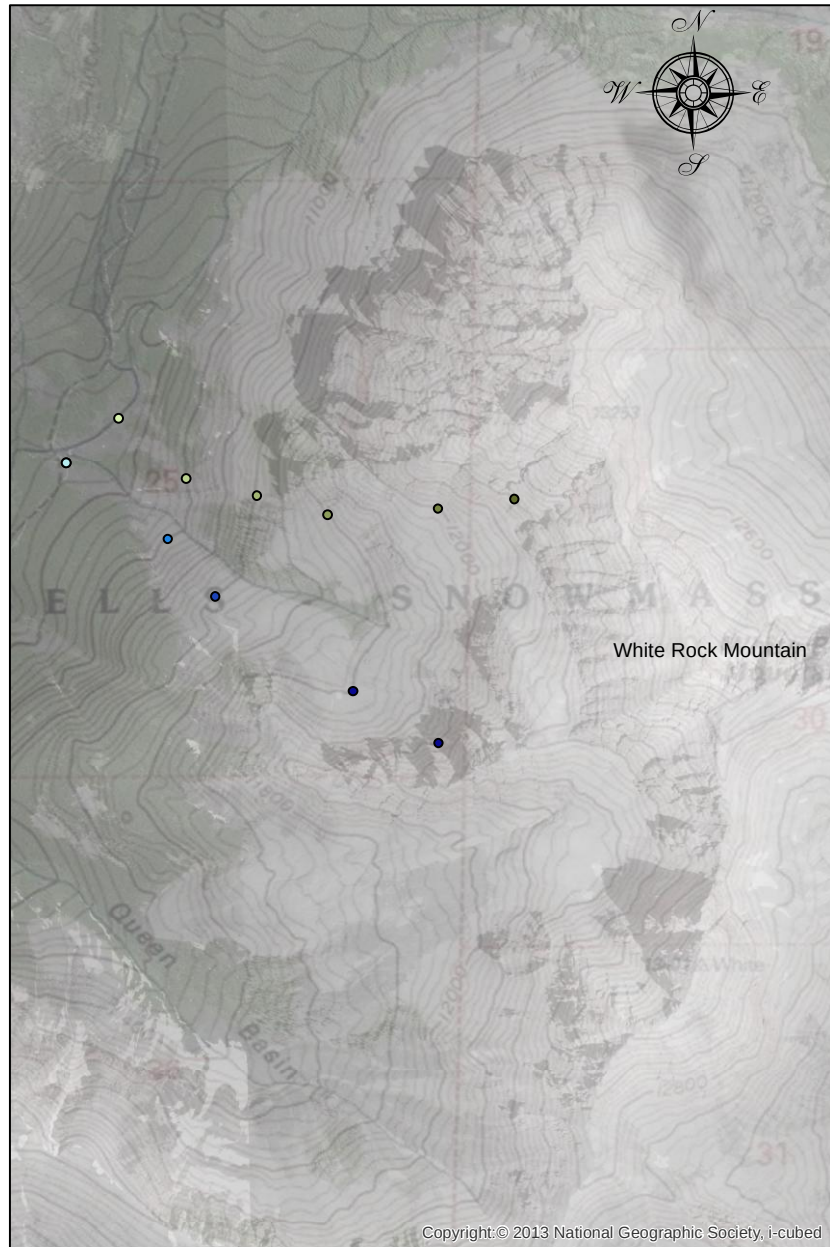
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White Rock Mountain Lichen Survey Sites



Legend

White Rock North **White Rock West**
Elevation (meters) **Elevation (meters)**

- | | |
|---------|-------------|
| ○ 10400 | ○ 10400 |
| ● 10800 | ● 10800.000 |
| ● 11200 | ● 11200 |
| ● 11600 | ● 11400 |
| ● 12000 | ● 12000 |
| ● 12400 | |

0 0.1 0.2 0.4 0.6 0.8
 Miles