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Vegetation change at high elevation: scale dependence and interactive effects on Niwot Ridge

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Abstract

Background: High-elevation mountain systems may be particularly responsive to climate change.

Aims: Here we investigate how changes along elevation gradients in mountain systems can aid in predicting vegetation distributional changes in time, focusing on how changing climatic controls affect meso-scale transitions at the lower and upper boundaries of alpine vegetation (with forest and subnival zones, respectively) as well as micro-scale transitions among plant communities within the alpine belt. We focus on climate-related drivers, particularly in relation to climate change, but also consider how species interactions, dispersal and responses to disturbance may influence plant responses to these abiotic drivers.

Results: Empirical observations and experimental studies indicate that changing climatic controls influence both meso-scale transitions at the upper and lower boundaries of alpine vegetation and micro-scale transitions among plant communities within tundra. Micro-scale heterogeneity appears to buffer response in many cases, while interactions between climate and other changes may often accelerate change.

Conclusions: Interactions with microtopography and larger edaphic gradients have the capacity to both facilitate rapid changes and reinforce stability, and that these interactions will affect the responsiveness of vegetation to climate change at different spatial scales.

Keywords: alpine tundra, biotic resilience, climate change, biodiversity, elevation gradients, microtopography, nitrogen deposition, Niwot Ridge LTER, snow distribution, treeline

Introduction

In high-elevation mountain ecosystems, plant populations and vegetation types are thought to be often strongly limited by climate-related factors (Harsch et al. 2009; Engler et al. 2011; Carlson et al. 2013). This strong control may cause these ecosystems to be particularly responsive to climate change; however, the very nature of tight climate control also predisposes the ecosystems to strong scale-dependent hierarchical dynamics. For instance, at the meso-scale (10–100 m), extratropical mountains are characterised by sharp elevation gradients that reflect a combination of temperature and precipitation gradients. Along smaller-scale topographic gradients (1–10 m), wind redistributes snow, slope and aspect affect temperature and radiation, and both temperature and radiation influence the timing of snowmelt. These scale-dependent and hierarchical drivers are essential to consider when predicting vegetation response to environmental change (Beniston et al. 1997; Körner 2004; Malanson et al. 2011; Rangwala and Miller 2012).

The alpine vegetation belt or alpine tundra zone in North America is defined at its lower boundary by the upper limit of upright trees (treeline) and at its upper limit by the limit of vascular plant life (tundra-subnival ecotone). Changes in these boundaries can be due to responses to climate at the meso-scale. For instance, upper treeline – the ecotone between alpine tundra and forest – has long been considered a sensitive proxy for the impact of climate variability on the distribution of high-elevation mountain forests (Körner 1998; Harsch et al. 2009; Malanson et al. 2011). Higher in elevation, the tundra-subnival ecotone is thought to be moving uphill as the climate warms (Gottfried et al. 2012; Pauli et al. 2012). Within the alpine tundra zone, climate and microtopography at smaller scales determine the distribution of particular alpine plant species and species assemblages (Kikvidze et al. 2005; Scherrer and Körner 2011; Spasojevic et al. 2013).

Typical of high-elevation mountain areas, Niwot Ridge on the Front Range in Colorado (40° 3' 20" N, 105° 35' 22" W) encompasses a complex elevation gradient from forest to treeline (at ca. 3400 m a.s.l.) to tundra to unvegetated subnival zones (often over 3700 m a.s.l.). Along this gradient, long-term records indicate that climate patterns are changing and that these changes vary with elevation. Climate stations in montane forest (e.g. C1 at Niwot Ridge; 3022 m a.s.l.) indicate increasing maximum temperatures, while higher in subalpine and alpine areas (e.g. D1, 3739 m a.s.l.); minimum temperatures have been increasing since the 1950s (McGuire et al. 2012). Concurrent increases have also been observed in total precipitation (Niwot LTER, unpublished data), particularly at higher elevations, with snowpack and temperature trends interacting to cause an earlier spring melt (Caine 2010; Clow 2010). Additionally, total N deposition rates are 6–8 kg N ha⁻¹ year⁻¹ (Sievering 2001) and have been increasing significantly over the last several decades (Williams and Tonnessen 2000; Mladenov et al. 2012). The site has been relatively free of direct anthropogenic disturbance apart from summer sheep grazing in the tundra prior to 1948 (Marr 1964) and timber

harvesting between 1900 and 1910 (Sibold et al. 2006). The most recent fire in the subalpine forest occurred around the turn of the twentieth century (Shankman 1984).

In addition to more recent changes in climate (documented since recording started in the 1950s), multiple environmental changes have occurred over the last thousand years, and likely to have contributed to modern vegetation patterns at Niwot Ridge. Late Holocene insect records show a progression from warmer-than-modern summers 900 years before present (BP) to cooler-than-modern summers during the Little Ice Age by 400 years BP (Elias 2001). Increased forb and grass pollen in regional subalpine pollen records during this cooling period has been interpreted as a lowering of treeline and a thinning of the subalpine forests (Short 1985; Vierling 1998). Glacial advances are thought to have reached their maximum extent by the mid-1800s, with a subsequent warming trend to modern-day climate.

In the seminal book on Niwot Ridge (Bowman and Seastedt 2001), Walker et al. (2001) described the abiotic drivers that strongly structure alpine tundra vegetation. Since then, many advances have been made in our understanding of the controls on tundra vegetation (e.g. Bowman et al. 2003; Seastedt et al. 2004; Ashton et al. 2008; Litaor et al. 2008; Meier and Bowman 2008) to the point that we can now begin to disentangle the primary drivers affecting alpine tundra vegetation and account for multiple scales of influence and hierarchical relationships among drivers. In this review, we investigate (1) meso-scale controls on forest-tundra and tundra-subnival ecotones as well as (2) micro-scale drivers of plant distribution within alpine tundra. We focus on climate-related drivers, particularly in relation to climate change, but also consider how species interactions, dispersal and responses to disturbance may influence plant responses to these abiotic drivers. We end with predictions concerning where and why we expect high sensitivity to environmental change in mountain systems.

Meso-scale distribution of subalpine (treeline) and subnival ecotones

The upper and lower boundaries that delimit the alpine tundra zone are best defined at the meso-scale (10–100 m), as ecotones in these high elevation landscapes are often defined by transitional zones rather than precise shifts (Körner 2012). Physiological responses to abiotic stress are thought to primarily shape species distributional limits, although there continues to be large uncertainty and debate about how to predict future responses based on these limits (Paulsen et al. 2000; Randin et al. 2009; Engler et al. 2011).

Lower boundary: the treeline ecotone

Globally, low temperatures are thought to limit tree growth above current treeline (Körner and Paulsen 2004; Körner 2012); thus, treeline is expected to shift up in elevation with climate warming. Tree establishment has increased substantially at the treeline throughout the southern Rocky Mountain region since 1950, leading to varying degrees of upslope treeline

advance (Malanson et al. 2007; Elliott 2011; Grafius et al. 2012). While there is substantial intra-regional variation, tree establishment over the twentieth century in the Front Range region was significantly correlated with increased summer temperatures and reduced snowfall (Holtmeier and Broll 2005; Elliott 2011). In many areas in the Front Range, simultaneous shifts in temperature and in tree establishment occurred between 1950 and 1954. This punctuated response may indicate that increasing temperatures that prolonged the growing season may have crossed a bioclimatic threshold in that period, enabling immediate increases in establishment (Elliott 2011; Elliott and Kipfmüller 2011).

Treeline surveys specifically focused on Niwot Ridge have found patterns similar to more regional trends (Shea 1985; Shankman and Daly 1988; Humphries et al. 2008), although they also highlight how interactions between climate and other factors control treeline dynamics. Perhaps more than other sites in the region, seedling establishment in the alpine tundra on Niwot Ridge appears to be strongly controlled by soil moisture and wind (Shea 1985; Humphries et al. 2008; Moyes et al. 2013). Age distributions indicate a relatively stable rate of establishment and persistence over time (Shea 1985), with fewer recruitment pulses than found regionally. Counts of seedlings above the treeline indicate frequent and persistent seedling establishment, including *Picea engelmannii* seedlings growing 50 m above the treeline in krumholz areas (Daly and Shankman 1985).

Geomorphology may locally modify large-scale temperature and precipitation influences (Malanson et al. 2007; Macias-Fauria and Johnson 2013). For example, solifluction lobes on Niwot Ridge create microtopography that could increase establishment along the edges of these lobes, where moisture is high and snow melt is early (Zeng et al. 2007). These lobes may be one cause for the vertical banding pattern of treeline seen in some areas across Niwot Ridge (Humphries et al. 2008).

A recent experiment on tree establishment at the treeline (the alpine treeline warming experiment; <https://alpine.ucmerced.edu/pub/htdocs/>) transplanted seeds and seedlings of two upper montane tree species, *Pinus flexilis* and *P. engelmannii* (Pinaceae), into common gardens at three sites on Niwot Ridge: below, at and above the current treeline. Seedlings of both tree species emerged at very low rates (<10%) in the present-day alpine tundra, with no *P. engelmannii* and very few (<2%) *P. flexilis* germinants able to survive past the end of the second season (Castanha et al. 2013). Emergence and survival were higher in the lower elevation sites, consistent with natural abundance patterns (Castanha et al. 2013). In addition to species comparisons, transplanted seedlings of two ecotypes of *P. flexilis*, one from low and one from high elevation, were compared to assess the importance of local adaptation. At all three elevations, seedlings from low elevation source populations had greater first and second year survival (Castanha et al. 2013), were bigger, invested more in aboveground growth and had greater photosynthesis rates than the high-elevation ecotype (Reinhardt et al. 2011).

Reinhardt et al. (2011) found that seedling growth was high even above the treeline and that growth was significantly correlated with photosynthesis and carbohydrate pools for both ecotypes. This physiological response may explain the success of the low-elevation population across the elevation gradient once dispersal limitation was circumvented.

In these same sites, plots were experimentally warmed with aboveground infrared heaters, with or without the addition of water to counter increased evaporation. Warming without the addition of water negatively affected *P. flexilis* because it increased seasonal moisture stress (Moyes et al. 2013). In 2010, seedling survival was greater in watered plus heated than heated only plots; warming was associated with reductions of first-year survival to as low as zero (Moyes et al. 2013). Survival also was negatively related to both the length and warmth of the growing season and to the number of days below a low moisture threshold (Moyes et al. 2013). Thus, even though soil moisture remained highest in the alpine tundra site, seedlings there experienced some degree of seasonal moisture stress, leading to reductions in carbon assimilation. That the most stressful conditions (high temperature and low moisture) occurred at the treeline site, which also experiences latest snowmelt, points to the combined importance of temperature and water in determining treeline expansion at Niwot Ridge. Higher temperatures that prolong the growing season may only facilitate upslope treeline movement given adequate soil moisture, either via snowmelt, high soil water-holding capacity of the site or high summer rainfall. If these patterns in seedling performance translate into long-term patterns in density, observed changes in treeline dynamics will be heterogeneous across the landscape (e.g. with aspect or slope position) and with inter-annual and decadal climate variability. These results also point to potential feedbacks, with tree establishment leading to greater snow retention (less redistribution due to wind), increased snowpack and greater soil moisture further promoting seedling establishment.

Upper boundary: the subnival ecotone

The transition areas from continuously vegetated alpine tundra to permanently snow/ice-covered areas higher in elevations (e.g. the upper alpine tundra line), variously termed subnival (Troll 1973) or periglacial (Karte 1983), are extremely patchy in their ability to support plant vascular life. Here, as in the transition from forest to tundra, the interaction between elevation, aspect and the prevailing winds (Erickson et al. 2005) is central to determining the distributions of organisms. Sheltered locations within the subnival zone harbour permanent snowfields surrounded by ephemerally sun-exposed, plant-free soils. Less sheltered locations downslope of snowfields are relatively habitable and support relatively continuous vegetation cover. Finally, wind-blown areas are dry and cold and support only low plant cover (King et al. 2012). Soil nutrients in subnival soils are, as a rule, extremely low and likely to accumulate nutrients only where environmental conditions are suitable for high microbial growth (Ley et al.

2004; King et al. 2010). Given a stable climate, this heterogeneous distribution of plants and microbially dominated barren soils is thought to be permanent over very long time scales (Troll 1973).

While we have only a basic understanding about changes in plant species composition along the upper limit of alpine tundra, both Walker et al. (1993) and Komarkova and Webber (1978) commented on lower representation of the plant communities that characterise high productivity areas (e.g. wet meadows) at higher elevation. Higher elevation alpine tundra areas are characterised by cooler temperatures and greater snowpack, which contribute to a general decrease of plant productivity with elevation (Komárkova and Webber 1978; Walker et al. 1993). Interestingly, Walker et al. (1993) found that west-facing slopes in the Front Range, which are generally wind-blown and support dry meadow and fellfield vegetation, are the one exception of this trend of lower productivity at higher elevation; west-facing slopes are unproductive regardless of elevation.

Several studies have found support for the prediction that plant species would generally move uphill into areas that were previously too harsh for plant life as the climate warmed (Gottfried et al. 1998, 2012; Pauli et al. 2007). However, variability in responses across mountain systems has caused some to challenge the assumption that climate change will cause a general uphill migration of plant species (Randin et al. 2009; Engler et al. 2011; Malanson et al. 2012). One reason for the call to refine the uphill migration paradigm is this evidence that alpine tundra plant species distributions are limited by a complex suite of environmental factors rather than solely by temperature (Callaghan et al. 2011; Gottfried et al. 2011); this suite of limitations may not translate easily to climate gradients (i.e. they may be azonal; Walter and Box 1976). For instance, after temperature-based constraints are removed, constraints associated with snowpack and moisture availability (Engler et al. 2011), soil nutrients (Litaor et al. 2008), nitrogen deposition (Seastedt and Vaccaro 2001; Bowman et al. 2012) and exposure (Walker et al. 1993; Erickson et al. 2005) may interact to influence elevational advance.

The plant species that currently grow at the extreme high-elevation sites (e.g. near Arikaree glacier in the Green Lakes Valley, 3830 m, Figure 1) are a subset of the alpine tundra species that characterise the more continuous alpine tundra at lower elevations (e.g. in the Saddle grid, Figure 1). In 2007, a spatially explicit nested grid of 160 plots, each 3 m² in size with spacing varying from 5 m to 2 km, was established along Niwot Ridge, into the Green Lakes watershed and up to the Arikaree glacier at the continental divide (King et al. 2010). Along this gradient, vegetation cover ranged from bare ground to complete cover (almost 100 stems per m²) and was partially related to elevation, soil nitrogen and snowpack patterns. As in the Saddle alpine tundra site, *Geum rossii*, *Deschampsia caespitosa* and *Kobresia myosuroides* were abundant plant species (King et al. 2012).

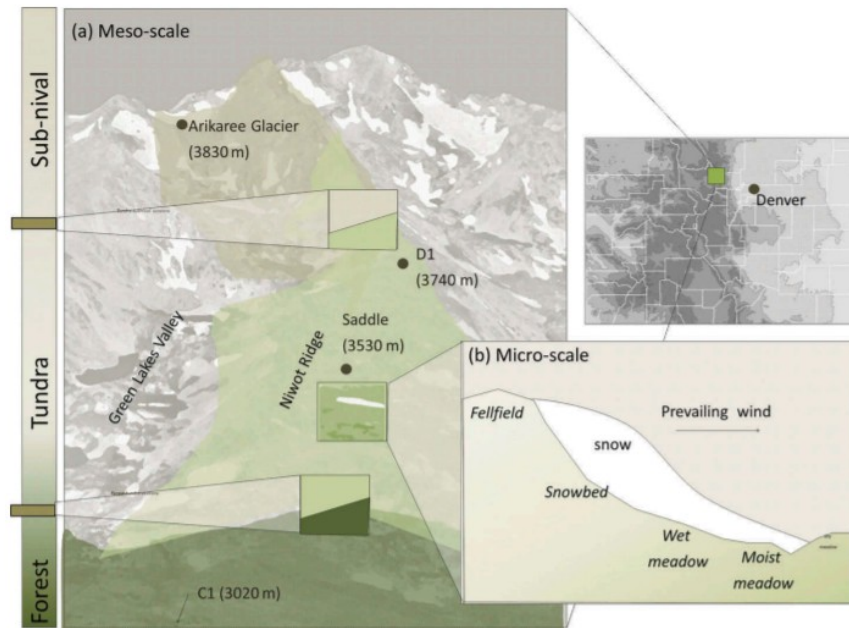


Figure 1. Typical of high-elevation mountain areas, Niwot Ridge on the Front Range in Colorado, USA ($40^{\circ} 3'-20' N$, $105^{\circ} 35'-22' W$) encompasses a complex elevation gradient from forest to treeline to alpine tundra to unvegetated subnival zones. (a) At the meso-scale (10–100 m), sharp elevational gradients that reflect a combination of temperature and snowfall gradients, and influence the distribution of vegetation types along forest–tundra and tundra–subnival ecotones. We note major research sites and their elevation (in metres above sea level) as well as the general distribution of vegetation types (forest, alpine tundra, subnival). (b) At a smaller scale (1–10 m), wind redistribution and topography also contribute to temperature and snowpack gradients, influencing the distribution of plant species within alpine tundra. Five plant community types are commonly described along these smaller-scale gradients (fellfield, snowbed, wet meadow, moist meadow, dry meadow). When predicting how vegetation will respond to environmental change, it is essential to consider scale dependency and hierarchical context.

Micro-scale distribution of plant species within alpine tundra

Within alpine tundra, microtopography can mimic temperature differences of large elevational (or latitudinal) gradients over very short horizontal distances. Specifically, patterns in temperature and the duration of snow cover reflect gradients in topography over short distances due to the redistribution of snow by wind (Seastedt et al. 2004). Thus, plant species have microtopographic niches within an altitudinal zone that reflect the very same environmental constraints (e.g. temperature, length of the snow period and snowmelt flow) that structure the larger altitudinal zonation patterns and lead to the formation of distinct community types (Walker et al. 1993, 2001). For example, snow accumulates on east-facing slopes, creating deep snowbeds that melt out late into the summer and harbour distinct plant species associations. Productivity is greatest in moist and wet meadow areas that melt out relatively early and are less constrained by growing season length but are downslope to receive snowmelt (Walker et al. 1994; Seastedt and Vaccaro 2001; Litaor et al. 2008). Areas where westerly winds blow free of snow receive little snowmelt and are the least productive areas (Walker et al. 1993). Due to the strong topographical variation of alpine landscapes, transitions among vegetation types can be sharp – gradients from high to low productivity can be 10 m or less in length (Spasojevic and Suding 2012).

The tight control of vegetation structure and composition by topographic factors has important consequences in the context of forecasting responses to climate change, and particularly to warming and changes in snowpack. Many studies in Europe have found that the alpine flora is moving up in elevation, likely as a result of climate warming (Grabherr et al. 1994; Walther et al. 2005; Jurasinski and Kreyling 2007; Lenoir et al. 2008; Parolo and Rossi 2008; Felde et al. 2012). However, variation in response to climate change may be due to the microtopographic niches that can either buffer or compound the effects of more regional climatic changes. In particular, models that take into account finer-scale environmental patterns find that heterogeneity can create refugia and resilience to climate change (Randin et al. 2009; but see Scherrer and Körner 2010; Rose and Malanson 2012), especially with respect to the large climatic differences between north and south-facing slopes.

Plant community composition within alpine tundra on Niwot Ridge appears to have been surprisingly stable over time. At the saddle grid, an area of alpine tundra relatively far from either the treeline or subnival ecotones (see Figure 1), a grid of 88 permanent 1 m² plots, was established over an 18 ha area to track changes in vegetation over time (described in Walker et al. 1993). Across seven surveys from 1989 to 2010, site-wide patterns indicate a slight but significant increase in species richness and diversity over time (Spasojevic et al. 2013). Increases occurred in all community types except in wet meadow for species richness; only the snowbed and moist meadow communities significantly increased in diversity (Shannon's index). Eighteen individual species increased in abundance over time, while four species exhibited significant decreases over time. While most plant responses were species-specific and not generalisable among functional groups or community types, mosses, lichens and soil crusts tended to decrease over time, shrubs tended to increase over time and snowbed communities were highly variable over time (Spasojevic et al. 2013).

The most notable vegetation change within the alpine tundra on Niwot Ridge has been the increase of native willow shrubs (primarily *Salix planifolia* Pursh and *S. glauca* L (Salicaceae); Johnson et al. 2011; Spasojevic et al. 2013), similar to observations in arctic tundra systems (Elmendorf et al. 2012). An examination of 10 aerial photographs spanning the period 1946–2008 indicated that *Salix* species have expanded by 441% over the 62-year period within the Saddle grid area on Niwot Ridge (from 0.24 to 1.29% cover; Formica et al. 2014). While small relative to the total carbon estimated in graminoid and herbaceous tundra vegetation (4123 kg ha⁻¹), the expansion corresponds to an increase in carbon storage of 168 kg ha⁻¹ (Formica et al. 2014). Drivers of the willow expansion remain unclear, with multiple interacting mechanisms likely. Many studies have correlated increases in alpine and arctic shrub cover and growth with increases in annual and summer temperatures (Cannone et al. 2007; Forbes et al. 2010; Hallinger et al. 2010; Van Bogaert et al. 2010), while other studies have pointed to the

importance of winter precipitation and snowpack (Wipf et al. 2009). In addition, the shrub increase may be a delayed recovery response to the high-intensity sheep grazing in the late 1940s (Olofsson et al. 2009; Brandt et al. 2013; Speed et al. 2013), but unfortunately no plant composition records exist prior to the grazing. Thus, we can only infer that this increase in shrubs is likely to be the result of interactions between climate and lack of grazing.

Long-term trends also suggest that snowbed communities might be more sensitive than other vegetation types to future changes in precipitation and snowmelt timing. Species not typical of snowbeds are colonising these areas in some years (Spasojevic et al. 2013), suggesting that these communities are very sensitive to variability in snow cover (Walker et al. 1994; Virtanen et al. 2003; Wipf et al. 2009). A recent modelling effort based on three sampling dates over a 30-year period at Niwot Ridge also suggested that snow bank vegetation was likely to decrease in the future (Johnson et al. 2011).

While environmental change is often thought to homogenise community composition, which may lead to lower rates of species turnover (beta-diversity) across space (Smart et al. 2006; Jurasinski and Kreyling 2007; Kuiters et al. 2009), we find little evidence of this dynamic at Niwot Ridge. The distribution of vegetation types has shifted through time, but these shifts were generally transient and only rarely translated into sustained directional changes of one vegetation type replacing another (Spasojevic et al. 2013). High microtopographic heterogeneity and interannual climate variability, with little directional changes in snowpack variability over time, may contribute to the relatively stable landscape diversity patterns.

Interactive drivers along gradients in climate

Several factors may influence how vegetation responds to climate-related drivers and could result in slower or faster than anticipated responses compared to considerations of climate alone (HilleRisLambers et al. 2013). Specifically, changes in nutrients, species interactions, dispersal and responses to disturbance may influence plant responses to climate-related drivers.

Changing nutrient limitation

Along with temperature and moisture, nutrients are another important factor structuring plant distribution. Although the alpine tundra is in general a low-nutrient system, nutrient availability varies within the alpine tundra zone, increasing from dry to moist to wet meadow communities (Bowman et al. 1993; Fisk et al. 1998). Considerable variation in soil N also exists within a community type due to species-specific effects on soil microbes and nutrient cycling processes through litter chemistry and root exudation. For example, in moist meadow the co-dominant *G. rossii* (Rosaceae) creates microsites with slow nutrient cycling rates, whereas under the other co-dominant *D.*

cespitosa (Poaceae) nutrient cycling is 4–10 times higher (Steltzer and Bowman 1998). This variation in nutrient availability at the patch scale has consequences for plant growth and reproduction, competitive ability and small-scale community structure (Bowman et al. 2004; Suding et al. 2004, 2006).

Increased anthropogenic N deposition may overwhelm existing heterogeneity in N and trigger large changes in vegetation (Bowman et al. 2012, 2014, this special issue). Nitrogen addition experiments at Niwot Ridge have shown that N alters community composition in all community types but in different ways: dry meadow diversity increases in response to N (likely because the dominant sedge *Kobresia* declines), whereas moist and wet meadow diversity declines sharply (likely related to the increase in abundance of the dominant grass *Deschampsia*) (Bowman et al. 1993, 2006; Theodose and Bowman 1997a). Although experiments added a fair amount of N in their manipulations, the critical loads measured for changing individual species abundance ($4 \text{ kg N ha}^{-1} \text{ year}^{-1}$) and for overall community change ($10 \text{ kg N ha}^{-1} \text{ year}^{-1}$) are quite low. This is well within the current rates of $6 \text{ kg N ha}^{-1} \text{ year}^{-1}$ (Williams and Tonnessen 2000) and near-future trajectories of N deposition (Dentener et al. 2006). Importantly, about half of the anthropogenic N inputs to the system occur in winter as snow which is redistributed by wind and melt out patterns on the landscape (Bowman et al. 1993), suggesting that some communities (i.e. snowbeds, wet meadows) might be experiencing ever greater N loads.

An ongoing *Salix* seedling transplant experiment indicated increased N and summer temperatures facilitate willow growth and increased snow increases survival, although N and N + snow together decreased survival (Formica et al. 2014). These results are consistent with the general finding that shrubs outcompete alpine tundra vegetation in warming manipulation experiments and at the lower boundaries of the alpine tundra (Walker et al. 2006; Elmendorf et al. 2012).

At the meso-scale, it is unclear how increased N deposition may affect the distribution of ecotones that define the alpine tundra zone. To the extent that the ecotones are also limited by nutrients, it may accelerate the advancement of both the tree limit and alpine tundra limit. Nitrogen fertilisation experiments at the forefront of glaciers in other subnival systems indicate a rapid increase in vegetation development associated with N (Knelman et al. 2014; Chapin et al. 1994); this may translate to increased rates of plant migration uphill with N deposition at Niwot Ridge. Distributional limits of treeline are often affected by soil moisture and geomorphology in addition to temperature (Grafius et al. 2012; Körner 2012); while we have not yet tested this prediction at Niwot Ridge, soil nutrients appear to play a lesser role.

Plant-species interactions

Facilitative and competitive interactions among plant species can influence the rate at which vegetation responds to abiotic factors (Pellissier et al. 2010). We expect several important effects of species interactions, both in determining the alpine ecotonal boundaries and species distribution within the alpine tundra zone.

At the treeline, spatially aggregated patterns of seedling establishment on Niwot Ridge are consistent with the expectation of positive biotic feedbacks (Humphries et al. 2008; Elliott and Kipfmueller 2011), particularly on south-facing slopes where moisture may be limiting and increased tree density may lead to greater snow retention (Elliott and Kipfmueller 2010). Sheltering by neighbouring trees and herbs also may reduce exposure of establishing seedlings to low-temperature induced photoinhibition, thereby increasing the efficiency of photosynthesis, in addition to increasing soil moisture (Maher et al. 2005). The importance of factors that modulate effects of climate on treeline tree establishment likely varies among species, with *Abies lasiocarpa* exhibiting most and *P. flexilis* least aggregation (*P. engelmannii* being intermediate) and benefits from neighbouring plants (Humphries et al. 2008). In addition, studies of tree seedling establishment above the tree limit at Niwot Ridge suggest that shrubs may facilitate tree establishment (Daly and Shankman 1985). It remains to be seen whether the expansion of shrubs into alpine tundra will facilitate tree establishment into higher elevations.

Facilitative interactions have been found in other alpine regions, particularly at higher elevations (Choler et al. 2001; Callaway et al. 2002; Butterfield et al. 2013). Removal of dominant species within the alpine tundra zone indicated that a mix of competitive and facilitative interactions predominate with competition among the dominant species (Theodose and Bowman 1997b; Suding et al. 2008), and facilitative interactions among particular dominant species (e.g. *G. rossii*) and rarer species (Suding et al. 2006). The effect of established species on recruitment appears to be generally negative, at least in the established areas of alpine tundra (Forbis 2009). Future work aimed at plant species interactions at the subnival ecotone would indicate whether facilitative interactions increase in frequency in higher elevation zones.

Indirect effects can occur due to responses of other species to abiotic factors. For example, N fertilisation (mimicking anthropogenic N-deposition) led to increased abundance of one abundant grass species, *D. caespitosa*, and community-wide drops in species diversity (Suding et al. 2006, 2008). Path analyses suggested that the drop in diversity was not a direct effect of N, but rather occurred as a result of competition with *Deschampsia*, which increased due to increased N (Farrer et al. 2015). Similar indirect effects via competitor abundance would be expected to occur with any abiotic driver that increases the abundance of dominant plant species; for instance, warming experiments also cause the increase of *Deschampsia*. In these cases, predicting diversity response to abiotic drivers will depend on

knowledge of the presence and interactions with dominant species, such as *Deschampsia*.

Plant-microbial interactions

Plant-microbial interactions have been found to influence the distributions of plants, both along ecotonal boundaries and within the alpine tundra zone (see Schmidt et al. 2014, this special issue). As work on plant-microbial interactions develops, evidence is accumulating to suggest that these interactions will also strongly influence plant response to abiotic drivers.

Plant-microbial associations may be an important factor in determining plant establishment in the low nutrient soils of the subnival zone. At the highest elevations near Arikaree glacier, arbuscular mycorrhizae were found at low levels in plant roots, and all plants sampled contained dark-septate fungi (Schmidt et al. 2008). Along an elevational grid that spanned between D1 and Arikaree (Figure 1), King et al. (2012) found a predominance of strong positive associations between plant species and bacterium taxa. These plant-bacterial associations were particularly strong in the most environmentally harsh areas of the subnival zone; experiments that manipulate the order of arrival of plants and microbes would be useful to demonstrate whether microbial communities limit plant establishment or whether plants foster particular microbial communities.

We know little about the role of microbial interactions at the treeline or in shrub expansion, but expect that microbial communities influence these vegetation patterns as well. Mycorrhizal associations may contribute to spatially aggregated patterns of seedling establishment, such as is found on Niwot Ridge, due to facilitation of seedling establishment by older trees at treeline (Hasselquist et al. 2005). While it appears that fungal associations may not limit the expansion of *Salix* shrubs into the alpine tundra, as root-associated fungal communities appear to closely associate with host species regardless of habitat (Becklin et al. 2012), the expansion of *Salix* may then facilitate ectomycorrhizal conifer establishment above the present treeline (Reithmeier et al. 2013).

While more is known about how microbial communities within the alpine tundra zone shift with abiotic drivers and nutrient availability (Schmidt et al. 2004; Nemergut et al. 2008) than how plant-microbial interactions shift with abiotic drivers, there is consistent evidence that alpine plants species associate with distinct bacterial and fungal communities (Haselwandter and Read 1980; Mullen and Schmidt 1993; Schmidt et al. 2000; Zinger et al. 2011; Farrer et al. 2013; Dean, Farrer, Taylor, et al. 2014; Schmidt et al. 2014). In one recent experiment, two abundant alpine tundra plant species (*D. caespitosa*, *G. rossii*) were found to support very distinct fungal and bacterial communities (with 10 and 17% operational taxonomic unit overlap, respectively; Dean, Farrer, Porrás-Alfaro, et al. 2014). N enrichment caused increased fungal, but not bacterial, diversity in the plant species that strongly declined at high N (*Geum*). Although the functions of most microbial

taxa at Niwot Ridge remain unknown (Schmidt et al. 2012), it may be that high N caused an increase in pathogenic fungi in the susceptible species.

Dispersal

Seed limitation may restrict the ability of plant species to readily track shifting habitats under climate change. We have very little quantification of dispersal limitation at Niwot Ridge, although work in other high mountain systems suggests the prevalence of seed limitation (Engler et al. 2009; Dullinger et al. 2012). Thus, while dispersal limitation likely will restrict the ability of plant species to track abiotic drivers, it is unclear how strong this limitation is, particularly with respect to other ecosystems (Carlson et al. 2013). Seed limitation may also cause the current plant distributions to not be in equilibrium with modern climate, but rather still responding to past climate change (Ives and Hansenbristow 1983; Elias 1996).

Work at the treeline ecotone suggests that dispersal may play a minor role relative to abiotic drivers. Transplant experiments of tree seeds below, at and above current treeline indicate survival patterns consistent with the current tree distribution, suggesting that seed limitation is not currently playing a large role in distributional patterns (Castanha et al. 2013). Complete recovery patterns following a fire at the turn of the twentieth century also suggest that the present-day treeline is not limited by seed availability (Shankman 1984).

Seed limitation is likely to be strong for many species within the alpine tundra zone (Forbis et al. 2004; Carlson et al. 2013). However, Forbis (2003) found seed recruitment at comparable levels to non-tundra systems, indicating that we should not expect seed limitation to be any greater here than in other systems. There has been little work on dispersal into the subnival zone at Niwot Ridge; work at other alpine-subnival ecotones also tends not to incorporate dispersal (Gottfried et al. 1999; Pauli et al. 1999, 2007).

Disturbance and herbivory

While climate can drive vegetation change, disturbance often provides the necessary prerequisite for rapid rates of change to occur due to lags between climate and vegetation response (Daniels and Veblen 2003). Peet (1981) suggested that the position of the upper tree limit in the Front Range is the result of a dynamic equilibrium between fire and climate, where frequent fire constrains the treeline reaching its true climatic upper limit. In contrast, Ives and Hansenbristow (1983) argued that the present forest-alpine ecotone is a relic of previously warmer climate, and recovery after disturbance will be slow or non-existent. Shankman (1984) found a high rate of tree establishment near the tree limit in areas burned in the early 1900s at Niwot Ridge, suggesting that the treeline here is persistent under modern climate conditions. In a regional study that included Niwot Ridge, Shankman and Daly (1988) also found continuous regeneration after fire at the upper

tree limit except in two sites where they speculate lack of seed dispersal (rather than climate) may limit recovery.

At the subnival zone, the major disturbances affecting vegetation are debris fall and substrate movement (Gottfried et al. 1998; Pauli et al. 1999). For instance, Gottfried et al. (1998) found that descriptors of the relative stability of substrate and microsites – relief curvature and roughness – explained more of the variability in vegetation composition than usual terrain attributes, such as elevation or exposure. In the context of this strong influence of disturbance, predictions of vegetation response in the subnival zone, including the uphill migration of plants due to warming, are often restricted to stable ridgelines rather than to the entire subnival zone (Pauli et al. 2007). While geomorphical activity at Niwot Ridge and adjacent Green Lakes Valley is considered modest compared to other high mountain areas, rates of soil erodability increase by orders of magnitude when vegetation cover is less than 25% in snowpatch sites (Caine 2010). A 25-year record in the upper Green Lakes Valley suggests that rockfall from the alpine cliffs yields about $12 \text{ m}^3 \text{ year}^{-1}$ of debris, a rather small amount compared to the existing volume of talus in the valley.

Looking forward

Scale dependency and interactive effects are proving to be essential constructs in a general understanding of vegetation change along the treeline to subnival elevational gradient at Niwot Ridge. We expect sensitivity to warming and snowpack trends in climate to be strongest at the meso-scale in two critical vegetation transitions: upper treeline to alpine tundra and alpine tundra to the subnival zone. However, in both cases, the underlying controls are not solely temperature-related changes along elevation gradients. Instead, we find repeated evidence of interactive controls of temperature and snowpack, mediated by microtopography, as well as interactive effects with biota and disturbance. Thus, we do not expect the changes in these ecotones to be consistent in either space or time. The interactions between smaller-scale microtopographical heterogeneity and larger-scale climate (temperature and snow) variability may also lead to complex patterns of change – discontinuous and abrupt dynamics – at these ecotones.

Interestingly, at the micro-scale, we found the vegetation types within the established alpine tundra to be relatively stable given substantial climate variation over recent decades. While the abundance of particular plant species have changed over time, there is little evidence that vegetation types within the alpine tundra – fellfield, dry meadow, wet meadow, for instance – are shifting in location or extent. It remains to be seen whether we will start seeing these transitions, for instance, from moist meadow to dry meadow, in future decades with stronger warming. Alternatively, tight topographic control may buffer the sensitivity to changed snowpack and temperature, at least up to a point where snowbeds and snowmelt patterns

dramatically change. The one large exception to this relative stability in intact alpine tundra is the rapid shrub encroachment; although, as mentioned above, it remains difficult to discern whether this increase is due to climate change or to a release from sheep grazing in the 1940s.

While many studies inform our understanding of vegetation structure and controls at Niwot Ridge, our ability to document changes over time has been limited to permanent plots set up at the Saddle grid area of the Ridge. While this location provides essential information about how core alpine tundra area is changing over time, this does not allow us to monitor changes in ecotone areas that we expect to be more sensitive than these core areas. Thus, in 2012 we added another component to our vegetation monitoring at the site: a series of six sites (one being the Saddle) that span an elevational gradient from treeline to the Arikaree glacier. At each site, 15 1-m² plots are arrayed across a snowpack gradient to enable detection of both changes due to changed winter precipitation within an elevational zone and changes across sites across elevation zones.

Finally, we expect that vegetation transitions at these ecotone areas will have strong effects on ecosystem processes. Net ecosystem exchange dramatically differs between subalpine forest and alpine tundra (Blanken et al. 2009; Knowles et al. 2014, this special issue). Forest development at treeline is likely to be associated with delayed snowmelt in the spring (Marks et al. 2008), with water and solutes infiltrating the soil and influencing stream biogeochemistry (Williams et al. 1998; Mladenov et al. 2012). In the subnival zone, vegetation transitions to alpine tundra will likely also have large consequences. Currently, the subnival areas are characterised by extremely high rates of nitrate export downhill, likely due to a combination of nitrogen deposition and microbial nitrification (Williams et al. 1997; Baron et al. 2009). Increased vegetation cover will likely act to reduce this export as plants take up N. The increase in soil organic matter and shading may act to reduce nitrifier abundance as well. While more work is needed to determine the ecosystem effects of these vegetation transitions, we expect that they will induce substantial change to both nutrient cycles and water balance if they occur.

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