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Abstract. One significant unanswered question about biotic responses to climate change is how plant communities within topographically complex landscapes will respond to climate change. Alpine plant communities are strongly influenced by topographic microclimates which can either buffer or compound the effects of more regional climatic changes. Here, we analyzed species changes over 20+ years in a complex alpine landscape with pronounced gradients in microtopography and consequently large variation in temperatures, snow depths, and nitrogen availability across small (10 m) scales. Using data from long-term monitoring plots from six community types, we asked how species composition and functional diversity changed over time in these different areas of the landscape, and whether fine-scale heterogeneity allowed species to move in response to temporal changes in the environment. We found site-wide patterns of increasing species and functional diversity. However, the majority of variability in composition over time was non-directional, both within and between community types. Within community types, *Carex*-dominated snow banks and wet meadow communities were the most variable in composition over time, while *Sibbaldia*-dominated snow banks, fellfield, dry meadow and moist meadow exhibited moderate change. Over forty percent of the plots also transitioned between community types during the census intervals, but these also were largely transient, with a shift occurring in one time interval and then shifting back in the next interval. Thus, even with evidence of directional change over time in climate, N deposition, and release from grazing, vegetation is tracking finer-scale variability both in time and space. Environmental heterogeneity may allow vegetation to track this finer-scale variability and enhance resilience to underlying directional changes in alpine and other topographically-complex environments.

Key words: alpine; climate change; Niwot Ridge Long Term Ecological Research site; plant functional traits; topography; vegetation change.

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INTRODUCTION

Mountain ecosystems, and particularly alpine ecosystems above treeline, are receiving much attention as systems particularly sensitive to climate change (Diaz et al. 2003, Korner 2003). Indeed, many studies have found that the alpine flora is moving upwards 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, 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 that alpine plant species distributions are limited by a complex suite of environmental factors rather than solely by temperature (Callaghan et al. 2011, Gottfried et al. 2012). Many alpine plant species are strongly limited by snowpack and moisture availability (Engler et al. 2011), with warming effects translating to stronger or weaker water limitation depending on the timing and amount of snowpack (Pauli et al. 2012). Alpine systems also can experience high levels of nitrogen (N) deposition (Baron et al. 2000, Williams and Tonnessen 2000, Weathers et al. 2006) and changes in land use associated with grazing (Quetier et al. 2007). N deposition can interact with warming to influence elevational advance (Bobbink et al. 2010, Smith et al. 2012). Grazing can strongly mediate vegetation response to climate change, often dampening the influence of warming (Klein et al. 2004, Speed et al. 2012).

In addition to this complex suite of environmental factors, alpine environments are characterized by fine-scale heterogeneity—often in the range of meters—that can mimic broader-scale environmental gradients in mountain ecosystems. Climatic patterns in temperature and the duration of snow cover are modified by pronounced gradients in topography over short distances, largely due to the redistribution of snow by wind (Korner 1995, Fisk et al. 1998, Seastedt et al. 2004) and solar radiation (Scherrer and Korner 2010). Within an altitudinal zone, plant species have microtopographic niches that reflect the very same environmental constraints

(e.g., temperature, length of the snow period, and snowmelt flow) that structure the larger zonation patterns and lead to the formation of distinct community types (Walker et al. 1993, Walker et al. 2001). Therefore, variation in response to climate change may be due to 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 demonstrate that heterogeneity can create refugia and resilience to climate change (Randin et al. 2009).

Thus, one expectation is that broader scale changes due to climate change, such as predicted upslope migration, may also be apparent within microtopographic gradients that also reflect these same climatic factors. For instance in a drier warmer climate scenario, at a fine scale, plants associated with drier fellfield communities might move down into areas previously dominated by species associated with wet or moist meadows. At a broader scale, these same fellfield species may be expected to move up elevation zones due to the decrease in snow-cover at higher elevations. Extending this expectation one step further, mountain systems with more fine-scale topographic heterogeneity may be more resilient to regional environmental changes because species can find local refuges where microtopography acts to buffer the regional climate changes (Scherrer and Korner 2010, 2011).

Some of the local scale-variation in response to global change factors may also occur because alpine tundra species do not respond in unison: species experience different environmental constraints and possess different life history strategies to respond to non-optimal conditions (Gross et al. 2009, Hillyer and Silman 2010, Pauli et al. 2012). While species diversity may not change within a given community type, as equal numbers of species are gained and lost, these lost and gained species should have different niche optima and thus differ in plant functional traits resulting in changes in functional diversity within a community. Alpine plant communities have been found to exhibit changes in functional composition with increasing productivity (increasing N-availability, temperature and soil moisture) including increases in plant height, leaf area, and chlorophyll content (Spasojevic and Suding 2012). This pattern suggests that

changes in N-availability, snow pack and temperature will likely lead to changes in the functional composition of alpine plant communities with a shift towards more resource acquisitive functional traits (e.g., taller, higher leaf area). These functional responses may also be apparent within an elevation zone across microtopographic gradients. For instance plants associated with dry meadow communities might move into areas previously dominated by species associated with snowbanks resulting in an increase in community mean height or leaf area.

Here, we analyzed species changes over time in a topographically complex alpine landscape with pronounced gradients in microtopography and consequently differential temperatures, snow depths, and nitrogen availability. At seven time points over a period of 21 years, we assessed species composition in permanent plots that ranged over seven community types arrayed by differences in microtopographic environmental constraints. We ask how species composition and diversity change over time in these different areas of the landscape, whether certain areas of the landscape are most sensitive to increasing temperatures and nitrogen deposition over time, and whether fine-scale heterogeneity allows species to move in response to temporal changes in the environment. We take both a taxonomic and functional approach to investigate these changes over time, as changes in functional attributes of plant species may be an ecological indicator of shifting environmental constraints and vulnerability of species (Hillebrand and Matthiessen 2009, Spasojevic and Suding 2012).

METHODS

Study site

This study was conducted in alpine tundra on Niwot Ridge (40°03′ N, 105°35′ W) which is located in the Front Range of the Colorado Rocky Mountains. Niwot Ridge has a short growing season (approximately 2–3 months) with a mean annual temperature of −2.2°C (6.4°C in the growing season) and an average annual precipitation of 884 mm, with the majority of the precipitation (94%) falling as snow (Litaor et al. 2008). Niwot Ridge annual daily wind speeds average 8.1 m s^{-1}, with an average annual daily maximum wind speed of 19.8 m s^{-1} (Losleben

and Chowanski, *unpublished data*).

Long-term climate measures at Niwot Ridge indicate that the alpine tundra is experiencing warmer minimum temperatures and wetter winters. Over the period of this study (1989–2010) minimum annual temperatures have increased by 0.43°C per decade (McGuire et al. 2012). Total precipitation has generally increased; mostly driven by changes in spring snowfall (Niwot LTER, *unpublished data*). However, these mean changes in temperature and precipitation are less than the interannual variability observed in these variables (Niwot LTER, *unpublished data*). Additionally, total N deposition rates are approximately 6–8 kg N ha^{-1} yr^{-1} (Sievering 2001), and have been increasing significantly over the last decades (Williams and Tonnessen 2000, Burns 2003).

An important structuring factor in alpine tundra is snow redistribution by wind (Greenland et al. 1984, Walker et al. 1993, Bowman and Fisk 2001, Williams et al. 2009). Wind keeps some areas snow-free all winter; these unproductive areas are characterized by temperature stress, low water availability, and low nitrogen availability (Billings and Mooney 1968, Walker et al. 2001). Areas where the blown snow accumulates, in contrast, are generally more productive (except snow bank communities), being buffered from wind scour and temperature stresses in the winter, and snow melt during the growing season enhances water and nitrogen availability. Soil moisture is significantly correlated with snowfall amounts and terrain factors that affect snow accumulation (Taylor and Seastedt 1994, Litaor et al. 2008). The redistribution of snow by wind and its effects on productivity, soil moisture, nutrient cycling and physical stress results in a mosaic of community types across alpine tundra landscapes. These community types include: barrens, dominated by lichens; fellfield, dominated by cushion plants and lichens; dry meadow dominated by xeric sedges and forbs, moist meadow, co-dominated by grasses and forbs; wet meadow, dominated by sedges and mesic forbs; late melting snow banks, dominated by forbs and sedges, and shrub tundra, dominated by shrubs (May and Webber 1982, Walker et al. 1993, Walker et al. 2001).

Field sampling

Eighty-eight permanent 1-m^2 plots were established in 1989 to track changes in vegetation over time. To quantify community composition in each plot point quadrat measurements were made at irregular intervals from 1989 to 2010 (1989, 1990, 1995, 1997, 2006, 2008, and 2010) using methods described by Auerbach (1992) for estimating canopy stratification and plant cover. Aluminum point-quadrat frames were 1-m^2 in size, with double-layer filament spaced 10 cm apart to make a 10×10 cm grid for a total of 100 sample points per plot. Before sampling, the point-quadrat frame was leveled and plots were aligned to permanent corner markers. For each hit at a sampling point, vascular plants were identified to species. Lichens and mosses were identified to species in 89–97 but not 06–10. In 90–97, only top and bottom canopy plant hits were recorded; in 89 and 06–10, middle hits were also recorded. We took several steps to ensure comparability in data across years. We only used "top" hits in all years, removing all middle hits from 89 and 06–10 data. All lichen and moss species recorded in 89–97 were classified as "lichen" or "moss" to maintain compatibility with 06–10 data. Lastly, data were examined for species identification consistency within each plot and species identities were changed where inconsistent species identifications across years were judged to be present.

Trait measurements

Community weighted mean trait values and functional diversity were calculated using species mean trait values from published trait data on plant height, specific leaf area, leaf area, stomatal conductance and chlorophyll content (Spasojevic and Suding 2012) collected as per Cornelissen et al. (2003). We chose these traits as they are generally correlated with resource availability and tolerance to environmental conditions. Plant height is often allometrically related to overall plant size (biomass, rooting depth, lateral spread) and competitive interactions for light (Westoby 1998, Aan et al. 2006, Vojtech et al. 2008) as well as facilitative interactions by blocking wind (Wilson 1959). Specific leaf area is associated with leaf life span and tissue N (Reich et al. 1997) and with an allocation strategy including fast relative growth rate and high photosynthetic capacity per unit leaf area (Westoby et al. 2002). Leaf area is associated with leaf energy and water balance, with heat stress, drought stress, cold stress and high-radiation stress tending to select for small leaf area (Cornelissen et al. 2003). Chlorophyll content is highly correlated with tissue N (Markwell and Blevins 1999). Stomatal conductance is indicative of water acquisition ability (Oberbauer and Billings 1981, Ehleringer and Marshall 1995). While we are unable to account for intraspecific trait variability amongst species found in multiple community types, this approach does provide a set of quantitative hypotheses to be addressed in future experiments.

Statistical analysis

To account for differing environmental habitat niches across the landscape grid, plots were classified into distinct community types for analysis. Groupings were conducted with a cluster analysis based on species cover values using Manhattan distance and Ward's clustering method in S-PLUS 6.1. All plots representing a barren community were dropped from the analysis because they either contained 100% rock or a mix of rock and lichen that was not identified to species. We dropped one plot that was identified as a separate community type in the cluster analysis because it was completely dominated by *Salix* spp. and had no replication. We also dropped two plots that were influenced by an ongoing snow manipulation. The resulting six community types were included in the analysis: fellfield (n = 8 in our first sampling period, 1989), dry meadow (n = 16), moist meadow (n = 22), wet meadow (n = 6), and two distinct snow bank communities: *Carex pyrenaica* (Cyperaceae)-dominated (n = 10) and *Sibbaldia procumbens* (Rosaceae)-dominated (n = 17). These groupings were consistent with previous treatments of the vegetation at the site (May and Webber 1982, Walker et al. 1993, Walker et al. 2001), except for the distinction between two snow bank types.

Our first analysis examined transitions between community types, focusing on areas of the landscape that are ecotonal in nature or at critical transition zones on the landscape. To examine transitions between different community types we reran the cluster analysis within each year of

the study after the first sampling (1989) and assessed if a given plot clustered with its community type from the previous year or clustered with a different community type which would indicate a transition among community types. We then classified transitions as either unidirectional, occurring once over the course of the sampling time period for a plot, or bidirectional, with a plot transitioning back and forth between community types over time, and used contingency analyses to ask whether these transitions were more likely to occur in particular areas of the landscape.

To further describe differences in community composition over time we used a non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity among plots in R (R Development Core Team 2010). Bray-Curtis dissimilarity is a semi-metric measure of dissimilarity used for continuous numerical data and does not group samples by shared zeros in the dataset (Beals 1984). "Stress" is a measure of departure from monotonicity in the relationship between the dissimilarity in the original n-dimensional space and distance in 2-dimensional ordination space (Kruskal and Wish 1978). In general, stress values <0.1 correspond to a good indication of the similarities between samples, whereas stress values >0.2 indicate a poor relationship (Clarke 1993). Stress values do not affect analyses conducted on dissimilarity matrices only how well the dissimilarity among sites is represented in a two dimensional figure (Clarke 1993). We used permutational analysis of variance (PERMANOVA: Anderson 2001) in the Vegan package (Oksanen et al. 2010) in R to test for differences in community composition among years within each community type (as defined by the cluster analysis, above). Permutational analysis of variance is very similar to an ANOVA but allows the analysis of differences in species composition rather than species numbers (Anderson 2001). We used indicator species analysis (Dufrene and Legendre 1997) to ask which species are driving significant differences in community composition over time within each community type. Thus, this second analysis focused on trends within a particular community type, rather than transitions between types.

To describe changes in richness and diversity over time we calculated species richness and

Shannon's diversity index for each plot in each community type in each year and calculated the average richness and diversity for each community type within each year. Species richness and diversity were calculated using the Vegan package (Oksanen et al. 2010) in R.

To describe changes in coarse functional groups we classified all species into the following groups: forbs, N-fixers, grasses, sedges (includes one species of rush), shrubs, cushion plants, mosses, lichens and soil crusts. We then summed the abundances of all species within each group for each community type to explore how these groups changed over time. Additionally, we describe changes in abundances of the species within each functional group within each community type (see Appendix: Table A1 for details).

To describe changes in functional composition and diversity over time we calculated mean community-weighted mean trait values and mean functional diversity within each community type in each year. Community-weighted mean trait values are a quantitative translation of the biomass ratio hypothesis (Grime 1998), calculated as the sum across all species of the products of each species trait value and their relative abundance (Garnier et al. 2004). We calculated functional diversity as functional dispersion (FDis) as per Laliberte and Legendre (2010). In multidimensional trait space, FDis is the mean distance of each species, weighted by relative abundances, to the centroid of all species in the community. While there are currently many metrics of functional diversity available (reviewed in: Mouchet et al. 2010, Schleuter et al. 2010), FDis was the most appropriate for our study because it is independent of species richness, takes into account species abundances, and can be used for single traits or multiple traits (Laliberte and Legendre 2010). For the analysis of CWM traits and FDis we did not have trait data on all species present in our dataset. Thus, we excluded any plots where we did not have trait data for the species that comprised the top 70% of relative abundance in a given plot (n = 52 plots for CWM and FDis analysis). Trait coverage was not high enough in any of the plots in the *Carex*-dominated snow bank community to include in this analysis; all other community types were analyzed. We lacked trait data for only three species that exhibited a significant change in

relative abundance (*Carex pyrenaica*, *Selaginella densa* var. *scopulorum*, and *Carex lachenalii*).

To determine how the measured diversity metrics (e.g., species diversity, CWM traits and FDis) changed over time we used a general linear model with time as a continuous variable and each diversity metric as a response variable. Each analysis was conducted separately within each community type (including any plots that transitioned into a community type in the year of and years after the transition) and across all community types to explore tundra-wide patterns. For each response measure, we tested for both linear and non-linear (unimodal) relationships. We selected the best fit using Akaike's Information Criteria (Crawley 2007).

RESULTS

Community (species) composition

The greatest similarities in community composition occurred among wet meadow and both snow bank communities (Fig. 1). Plots designated as dry meadows were most distinct from other plots in composition, with fellfield and wet meadow plots also clustering very tightly by
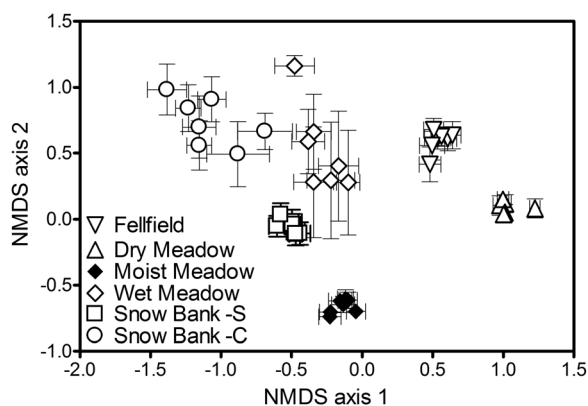

Fig. 1. Differences in community composition among plots classified into the six community types over the seven census years. Each symbol indicates the mean NMDS scores (±SE) over all plots classified as a given community type in a given year. Symbols closer to each other are more similar to each other than those further apart. While wet meadow and snow bank–*Carex* communities show the most temporal variation in community composition, this variation was not directional over time (see Fig. 2). Stress = 0.19.

themselves in terms of composition.

We identified 46 instances where a plot changed classifications over the study period (Fig. 2). Twenty-two (28%) of the plots transitioned between two community types at least once in the study and of these plots, over 75% of the plots (16 of 22) did so more than once, going back and forth between two community types. Many (5 plots) transitioned more than two times (e.g., A to B, B to A, A to B), indicating non-directional inter-census shifts, but no plot transitioned between more than two community types. The majority of the single unidirectional transitions occurred between 1989 and 1990 (5 of 6), the first sampling interval, and were from a wetter more snow-dominated community to a drier community type. The number of multiple transitions has increased over time, with the most common bi-directional transitions occurring between one of the snowbed communities (dominated by *Carex*) and either wet meadows or the other snowbed type. Moist meadows and fellfields, while very distinct in composition (Fig. 1), exhibited a consistently low rate of transitions to other community types (about 10% per interval). None of the plots classified as dry meadows in the 1989 census changed classification during the census intervals.

While none of the dry meadow plots transitioned to other community types according to cluster analysis, composition in dry meadow communities significantly differed over time ($F_{6, 104} = 2.67$, $P < 0.001$, Fig. 3). Indicator species analysis showed that the differences in community composition among years were correlated with changes in several species including decreasing abundances of *Kobresia myosuroides* (Cyperaceae), *Bistorta bistortoides* (Polygonaceae), and *Thlaspi montanum* (Brassicaceae) and increasing abundances of *Festuca brachyphylla* (Poaceae), *Lloydia seotina* (Liliaceae), *Sedum lanceolatum* (Crassulaceae), *Campanula uniflora* (Campanulaceae), *Minuartia obtusiloba* (Caryophyllaceae), and *Erigeron simplex* (Asteraceae). The other communities exhibited changes in composition over time but these changes were non-directional (fellfield: $F_{6,62} = 1.11$, $P = 0.28$; moist meadow: $F_{6, 155} = 1.54$, $P = 0.15$; wet meadow: $F_{6, 27} = 0.66$, $P = 0.88$; *Carex*-dominated snow bank: $F_{6,50} = 0.97$, $P = 0.51$; and *Sibbaldia*-dominated snow bank: $F_{6, 115} = 0.90$, $P = 0.34$). For dry meadows, the largest
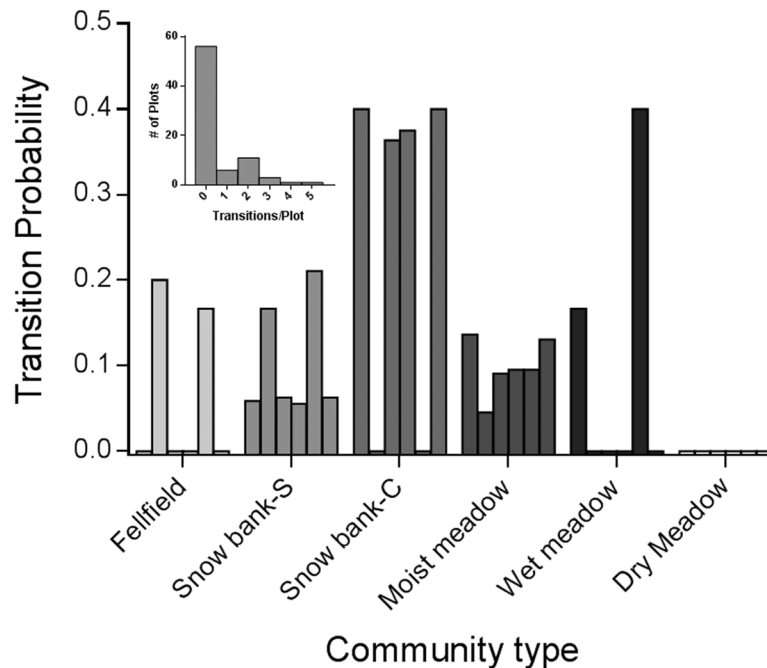
Fig. 2. Probabilities of plots transitioning from one community type to another (as defined by cluster analysis and shown in Fig. 1) between census intervals. For a given community type, each bar represents a time interval, ordered earliest to latest: 1989–1990, 1990–1995, 1995–1997, 1997–2006, 2006–2008, 2008–2010. Transitions are described by initial community type designation, and are calculated as the number of transitions relative to the number of total plots of that designation. Inset: Histogram describing the number of times a plot transitioned to another type, with 0 indicating that the plot never transitioned over the course of the surveys.

composition change occurred between 1989 and 1990 censuses, consistent with the large number of unidirectional transitions occurring between other community types during that time interval as well.

Species richness and diversity

We found a tundra wide pattern of increasing richness and diversity over time ($F_{1,6} = 11.74$, $r^2 = 0.64$, $P = 0.02$; and $F_{1,6} = 19.11$, $r^2 = 0.75$, $P = 0.007$, respectively) and variable responses among community types (Fig. 4). In the fellfield, diversity significantly increased over time ($F_{1,6} = 22.44$, $r^2 = 0.78$, $P = 0.005$) but not species richness ($F_{1,6} = 3.71$, $P = 0.12$). In the dry meadow, the number of species increased with time ($F_{1,6} = 17.48$, $r^2 = 0.73$, $P = 0.008$), but that was not reflected in the change in diversity over time ($F_{1,6} = 2.92$, $P = 0.15$), suggesting a decrease in evenness over the same period, probably due to decreases in abundance of the dominant *Kobresia*. Neither richness or diversity significant-

ly changed over time in the moist meadow community ($F_{1,6} = 1.75$, $P = 0.24$; and $F_{1,6} = 1.41$, $P = 0.29$, respectively), the *Carex*-dominated snow bank ($F_{1,6} = 1.46$, $P = 0.28$; and $F_{1,6} = 2.92$, $P = 0.15$, respectively), or the wet meadow community ($F_{1,6} = 0.6$, $P = 0.81$ and $F_{1,6} = 0.01$, $P = 0.97$, respectively). Lastly, both species richness and diversity increased over time in the *Sibbaldia*-dominated snow bank ($F_{1,6} = 33.86$, $r^2 = 0.84$, $P = 0.002$; and $F_{1,6} = 10.77$, $r^2 = 0.62$, $P = 0.02$, respectively).

Life form

Changes in the abundance of different life forms varied by community type and by life form (Table 1). Generally, moss, lichens, and soil crusts were found to decrease or show no response over time in the different community types (Table 1). As a group, neither forbs nor grasses showed any significant change over time (Table 1). However, many individual species changed in abundance over time (Appendix: Table A1). N-fixers de-
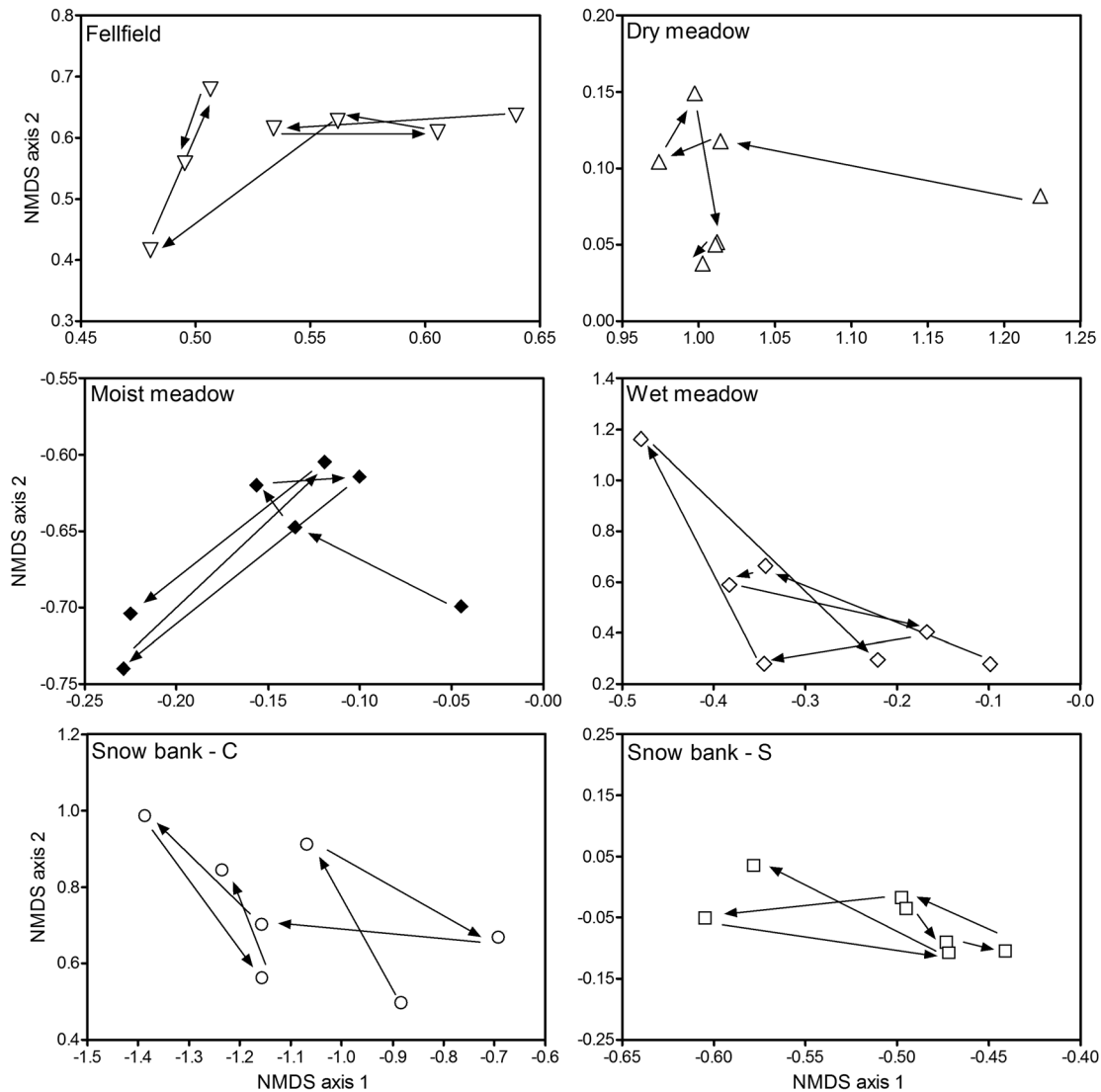
Fig. 3. Changes in community composition over time for each community type. Arrows indicate direction of change over time. Note different scales of axes. Dry meadow and moist meadow communities showed directional change in composition over time; however the degree of change varied among community types with dry meadow showing the greatest directional change. Fellfield, wet meadow, and both snow bank communities fluctuated in composition over time, but did not exhibit directional change. Because plots were classified by cluster analysis year by year, compositional factors contributing to the groupings were not held static and were allowed to change each year. Error bars omitted for clarity. Stress = 0.19 for all community types.

creased in abundance in *Sibbaldia*-dominated snow bank and increased in dry meadow communities (Table 1). Shrubs increased in abundance in moist and wet meadow communities, but not in dry meadow or fellfield (Table 1). Cushion plants increased in abundance over time in dry meadow, moist meadow and *Sibbaldia*-

dominated snow bank communities. Sedges were found to increase in fellfield and *Sibbaldia*-dominated snow bank communities (Table 1). Across all community types we found a tundra-wide pattern of increasing abundance of shrubs and cushion plants ($F_{1,6} = 200.61$, $r^2 = 0.97$, $P < 0.001$; and $F_{1,6} = 17.45$, $r^2 = 0.73$, $P = 0.008$,
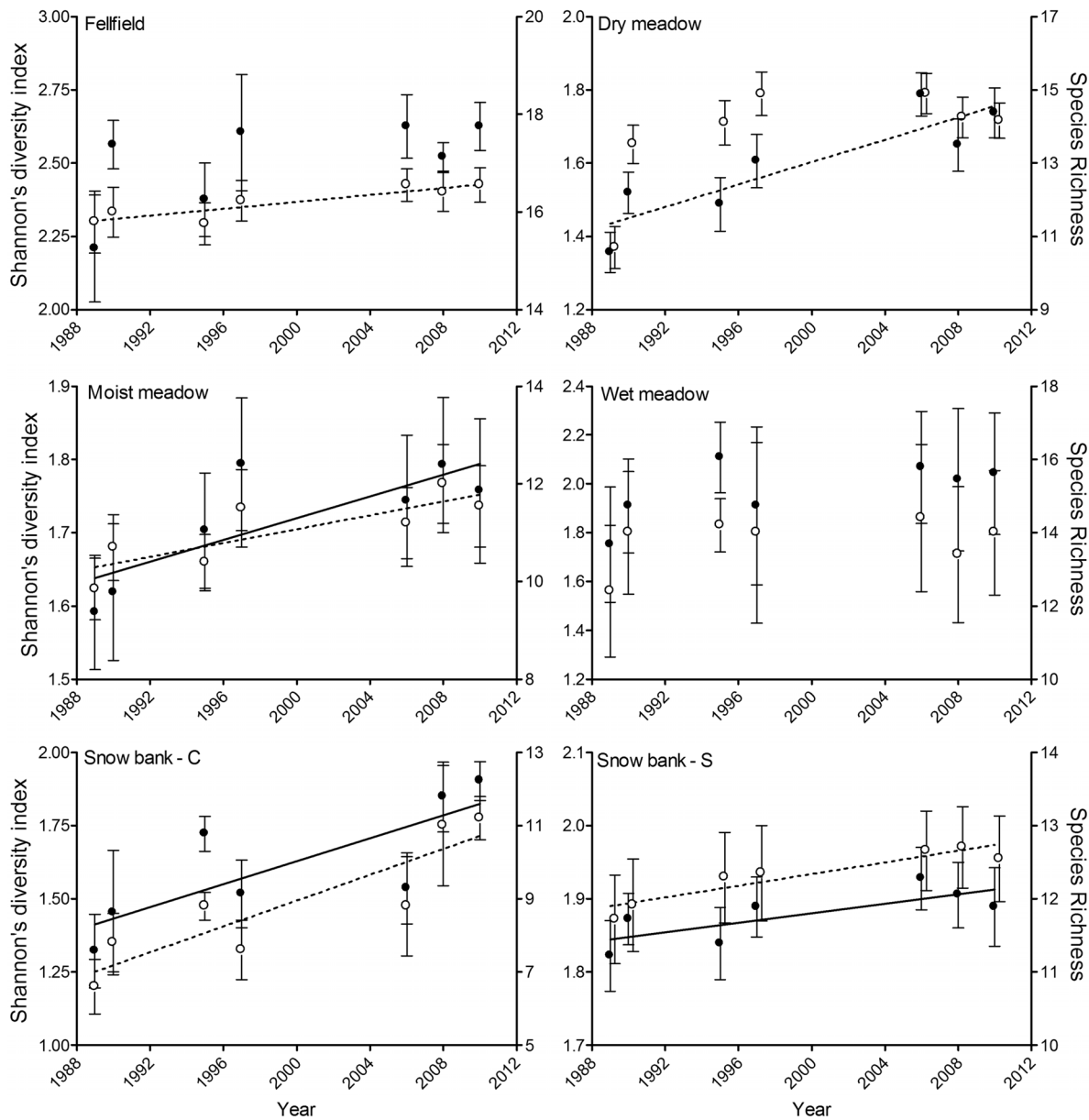
Fig. 4. Changes in diversity (H′, black circles, solid lines) and species richness (no. species, white circles, dashed lines) per m² over time for each community type. Note different scales of axes. Only significant relationships are shown. Overall, richness and diversity significantly increased over time.

respectively) and a decrease in mosses over time ($F_{1,6} = 7.68$, $r^2 = 0.53$, $P = 0.04$). None of the other life forms showed tundra wide patterns of change over time.

Community weighted mean trait values

The fellfield, dry meadow and wet meadow communities exhibited stable functional trait composition over time (Table 2). Compositional changes in the moist meadow and *Sibbaldia*-dominated snow bank communities were related to increases in mean SLA, and decreases in mean leaf area and mean chlorophyll content (Table 2). Additionally, across all community types we

Table 1. Change in abundance of different plant life forms in each community type over time. Negative slope values represent a negative relationship and positive slope values indicate a positive relationship. n.s. indicates non-significant relationships, *P < 0.05, **P < 0.01, ***P < 0.001.

Life form	Slope	r^2	F
Fellfield			
Forb	n.s.	n.s.	n.s.
N-fixer	n.s.	n.s.	n.s.
Grass	n.s.	n.s.	n.s.
Sedge	+0.22	0.52	7.39*
Shrub	not present		
Cushion	+0.24	0.69	14.37*
Lichen	−0.61	0.71	15.95*
Moss	n.s.	n.s.	n.s.
Soil crust	n.s.	n.s.	n.s.
Dry meadow			
Forb	n.s.	n.s.	n.s.
N-fixer	+0.13	0.86	40.28**
Grass	n.s.	n.s.	n.s.
Sedge	n.s.	n.s.	n.s.
Shrub	+0.04	0.91	61.75**
Cushion	+0.06	0.73	17.44**
Lichen	n.s.	n.s.	n.s.
Moss	n.s.	n.s.	n.s.
Soil crust	n.s.	n.s.	n.s.
Moist meadow			
Forb	n.s.	n.s.	n.s.
N-fixer	n.s.	n.s.	n.s.
Grass	n.s.	n.s.	n.s.
Sedge	n.s.	n.s.	n.s.
Shrub	+0.04	0.88	46.18**
Cushion	+0.11	0.80	25.04**
Lichen	−0.11	0.48	6.66*
Moss	n.s.	n.s.	n.s.
Soil crust	n.s.	n.s.	n.s.
Wet meadow			
Forb	n.s.	n.s.	n.s.
N-fixer	n.s.	n.s.	n.s.
Grass	n.s.	n.s.	n.s.
Sedge	n.s.	n.s.	n.s.
Shrub	+0.32	0.79	23.30**
Cushion	n.s.	n.s.	n.s.
Lichen	n.s.	n.s.	n.s.
Moss	n.s.	n.s.	n.s.
Soil crust	−0.06	0.56	8.63*
Snow bank–C			
Forb	+0.66	0.83	31.70**
N-fixer	n.s.	n.s.	n.s.
Grass	n.s.	n.s.	n.s.
Sedge	n.s.	n.s.	n.s.
Shrub	not present		
Cushion	+0.05	0.52	7.51*
Lichen	−0.04	0.75	18.54**
Moss	−0.95	0.85	34.31**
Soil crust	n.s.	n.s.	n.s.
Snow bank–S			
Forb	n.s.	n.s.	n.s.
N-fixer	−0.29	0.57	9.09*
Grass	+0.14	0.66	13.04*
Sedge	+0.20	0.94	91.01***
Shrub	not present		
Cushion	+0.13	0.51	7.26*
Lichen	n.s.	n.s.	n.s.
Moss	n.s.	n.s.	n.s.
Soil crust	n.s.	n.s.	n.s.

Table 2. Changes in multivariate functional diversity and in community weighted mean (CWM) trait values in each community type. Negative slope values represent a negative relationship between community-weighted mean traits and time and positive slope values indicate a positive relationship. n.s. indicates non-significant relationships, *P < 0.05, **P < 0.01, ***P < 0.001.

Trait metric	Slope	r^2	F
Fellfield			
Multivariate functional diversity	n.s.	n.s.	n.s.
CWM Height	+0.04	0.47	6.54*
CWM SLA	n.s.	n.s.	n.s.
CWM Leaf area	n.s.	n.s.	n.s.
CWM Stomatal conductance	n.s.	n.s.	n.s.
CWM Chlorophyll content	n.s.	n.s.	n.s.
Dry meadow			
Multivariate functional diversity	n.s.	n.s.	n.s.
CWM Height	n.s.	n.s.	n.s.
CWM SLA	n.s.	n.s.	n.s.
CWM Leaf area	n.s.	n.s.	n.s.
CWM Stomatal conductance	n.s.	n.s.	n.s.
CWM Chlorophyll content	n.s.	n.s.	n.s.
Moist meadow			
Multivariate functional diversity	+0.0006	0.84	32.41**
CWM Height	n.s.	n.s.	n.s.
CWM SLA	+0.23	0.66	12.80**
CWM Leaf area	−0.02	0.69	14.73*
CWM Stomatal conductance	n.s.	n.s.	n.s.
CWM Chlorophyll content	−0.94	0.57	9.16*
Wet meadow			
Multivariate functional diversity	n.s.	n.s.	n.s.
CWM Height	n.s.	n.s.	n.s.
CWM SLA	n.s.	n.s.	n.s.
CWM Leaf area	n.s.	n.s.	n.s.
CWM Stomatal conductance	n.s.	n.s.	n.s.
CWM Chlorophyll content	n.s.	n.s.	n.s.
Snow bank–S			
Multivariate functional diversity	+0.0008	0.65	12.53**
CWM Height	n.s.	n.s.	n.s.
CWM SLA	+0.55	0.76	20.58**
CWM Leaf area	−0.03	0.81	27.71**
CWM Stomatal conductance	n.s.	n.s.	n.s.
CWM Chlorophyll content	−2.88	0.92	74.33***

found a tundra wide pattern of increasing community weighted mean SLA ($F_{1,6} = 10.96$, $r^2 = 0.62$, $P = 0.02$) and decreasing leaf area and chlorophyll content over time ($F_{1,6} = 63.52$, $r^2 = 0.91$, $P < 0.001$; and $F_{1,6} = 7.74$, $r^2 = 0.53$, $P = 0.04$, respectively). Community weighted mean height exhibited a marginally significant trend toward greater height over time ($F_{1,6} = 4.10$, $P = 0.09$) and stomatal conductance did not significantly change over time ($F_{1,6} = 1.60$, $P = 0.21$).

Functional diversity

We found that multivariate functional diversity increased over time in the moist meadow ($F_{1,6} = 32.42$, $r^2 = 0.84$, $P = 0.002$) and *Sibbaldia*-dominated snow bank ($F_{1,6} = 12.55$, $r^2 = 0.66$, $P = 0.01$) communities. There was no significant change in functional diversity over time in the fellfield ($F_{1,6} = 2.60$, $P = 0.16$), dry meadow ($F_{1,6} = 0.80$, $P = 0.41$), or wet meadow ($F_{1,6} = 0.00$, $P = 0.99$) communities. Additionally, across all community types we found a tundra-wide pattern of increasing functional diversity over time ($F_{1,6} = 21.22$, $r^2 = 0.77$ $P = 0.006$).

DISCUSSION

While recent studies suggest that tundra communities are changing in response to global change (Johnson et al. 2011, Elmendorf et al. 2012, Gottfried et al. 2012, Pauli et al. 2012), tundra communities within topographically complex landscapes, such as alpine tundra, may be more resilient to change than previously thought (Randin et al. 2009, Scherrer and Korner 2010, 2011). Despite changes in temperature (McGuire

et al. 2012), N deposition reaching critical loads (Bowman et al. 2006), and changes in precipitation patterns (Niwot LTER, *unpublished data*), our results suggest community composition at Niwot Ridge has been surprisingly resilient to these directional changes over a twenty year period. Transitions between community types were frequent across the seven time points of measurement, but these shifts were generally transient and often did not translate into sustained directional changes. We attribute this community resilience to a combination of microtopographic heterogeneity and interannual climate variability.

Superimposed on these patterns driven by temporal and spatial heterogeneity, however, we also found site-wide patterns of increasing species richness, taxonomic diversity and functional diversity. These results are in contrast to the general expectation that climate change and/or land use change will lead to a decrease in diversity and richness due to increased strength of biotic interactions or increased maximum temperatures (McLaughlin et al. 2002, Thomas et al. 2004, Thuiller et al. 2005, Barnosky et al. 2011). The increase in diversity and richness we found are likely a result of directional environmental change relaxing the strong environmental filtering in alpine tundra. While alpine plants are well adapted to their "harsh" environment, environmental filtering (minimum temperatures, wind) generally restrict non-alpine species from establishing in alpine tundra (Billings and Mooney 1968, Korner 2003). More recent directional environmental change is leading to an upslope movement of tundra and non-tundra plant species in many locations around the world (Lenoir et al. 2008, Felde et al. 2012) and may be permitting the persistence of a wider range of functional strategies (increased functional diversity) and in turn higher numbers and a greater diversity of species (e.g., the physiological tolerance hypothesis: Currie et al. 2004) due to the relaxation of this "strong" environmental filtering. While abiotically structured environments such as alpine may first experience an increase in diversity with directional climate change due to the range expansion of species previously unable to establish, longer-term directional change may decrease diversity as alpine species lose optimal habitat as increasing temperature shift their niche optimum further and

further up slope (Gottfried et al. 2012, Pauli et al. 2012).

While these site-wide patterns indicate the potential for overall change, our results also suggest that potential changes at the community level will differ strongly among community types with some community types changing more than others. The two snow bank communities exhibited the greatest changes in community composition over the study period. The *Carex* snow bank community exhibited the most variation in community composition over time and the greatest probability of transitioning community types. The *Sibbaldia* snow bank community was the only community type to show changes in both species diversity and richness (suggesting species gain, as opposed to changes in abundance) and the most change in functional diversity and CWM trait values. This increased responsiveness of snow bank communities may reflect that these communities are strongly influenced by variability in snow cover (Walker et al. 1994, Galen and Stanton 1995, Sandvik et al. 2004, Wipf et al. 2009) and suggest that they may be more susceptible to longer term changes in winter precipitation. Similarly, a recent modeling effort based on three sampling dates of vegetation data taken over a thirty year period at this site suggests that the prevalence of snow bank vegetation will decrease in the future (Johnson et al. 2011).

Wet meadow communities appear to be the least responsive to change over the 20+ years that these plots have been monitored. Within this community type, there was no change in species diversity, species richness, or functional diversity over time. The only changes observed were an increase in shrubs and a decrease in soil crusts. As these communities are typically found in low-lying areas that accumulate water (Walker et al. 2001), changes in the timing of snow melt or the amount of snow may not be as critical for these communities as in the snow bank community types. Additionally, the often saturated soils in this community type may serve as an additional abiotic filter and restrict other alpine species from moving into this community type, especially any species from drier habitats.

The other three community types, fellfield, moist meadow and dry meadow, exhibited moderate change over the last twenty years.

Fellfield communities experienced an increase in diversity (Fig. 4) and a concurrent increase in sedges and cushion plants and a decrease in lichens (Table 1) resulting in an increase in community weighted mean height (Table 2).We found that the moist meadow communities had relatively low probabilities of transitioning between community types and had no change in richness or diversity over time, supporting the modeling efforts of Johnson et al. (2011). However, this community exhibited more change in functional traits than most other communities; functional diversity and CWM SLA increased over time while CWM leaf area and chlorophyll content decreased. These changes in traits may be driven by a decreasing abundance the community dominant *Geum rossii* (a species with low SLA) allowing an increase in species with higher SLA (Appendix: Table A1). On the other hand, dry meadow communities experienced a shift in composition (Fig. 3) and an increase in richness (Fig. 4) resulting from an increase in shrubs, cushion plants and N-fixers (Table 1). Dry meadow and moist meadow communities have been found to be particularly responsive to N fertilization in experiments and the long term trends generally match experimental results for these two community types. In moist meadows, N-fertilization did not affect richness but did cause a strong decline in one of the co-dominant species *Geum rosii* (Roseaceae) (Suding et al. 2008). Our results suggest similar patterns, no change in richness and a strong decline in *Geum rosii*. Results from a N-fertilization experiment in dry meadow tundra found no change in richness, but an increase in taxonomic diversity and a shift in community composition due to increasing abundances of *Carex rupestris* (Cyperaceae) and *Trisetum spicatum* (Poaceae) and decreasing biomass of dominant *Kobresia myosuroides* as a result of N enrichment (Bowman et al. 2006). In our dry meadow community plots we found an increase in richness, no change in diversity and a shift in composition partially due to a decrease in *Kobresia myosuroides* (as suggested by the indicator species analysis). Our results are consistent with a signature of N-enrichment in moist meadows, but suggest that N-enrichment may be interacting with other factors to influence dry meadow communities.

Indeed, these interactions among environmental and biotic factors are predicted to strongly influence changes in species composition and ecosystem function (Heimann and Reichstein 2008, Luo et al. 2008, Rustad 2008) and may be especially important in tundra ecosystems (Chapin et al. 1995). The increase in shrubs found in all communities where shrubs are present at Niwot Ridge (Table 1) may be a result of an interaction between climate change and grazing. Niwot Ridge was regularly grazed by sheep and cattle before 1946 (Marr 1964; Benedict, *unpublished data*) and the observed expansion of shrubs may be the gradual recovery of woody vegetation from a history of grazing. However, little growth occurred in the three decades immediately following grazing cessation and shrubs may be increasing due to interactions among global change factors which may be reinforced by positive snow-N cycling feedbacks generated by willows themselves (K. N. Suding, *unpublished data*). This increase in shrubs has the potential to drastically change the tundra community, decrease albedo and creating positive feedbacks with climate change (Myers-Smith et al. 2011).

Across Niwot Ridge diversity is increasing (taxonomic richness and diversity as well as functional diversity) likely due to multiple factors. The increase in minimum temperatures, winter precipitation and N-deposition seen at this site over the last 20 years (Williams and Tonnessen 2000, Burns 2003, Caine 2010) likely contribute to this increase in diversity by allowing species to expand into other community types. While alpine species are well adapted to the "harsh" alpine environment (Korner 1995, 2003), increased favorability in environmental conditions may allow less well adapted species to increase in abundance (i.e., the physiological tolerance hypothesis: Currie et al. 2004). Shrubs and many forb and grass species may be able to take advantage of the longer growing season and warmer temperatures (more favorable environmental conditions), at the expense of mosses. Additionally, changes in these global change factors have the potential to alter species interactions (Klanderud 2005, Klanderud and Totland 2005, Crabtree and Ellis 2010) resulting in changes in diversity mostly due to rarer plants establishing and perhaps starting to spread. For example, in moist meadows, the co-dominant in this community type *Geum rossii* (Roseaceae) is

decreasing and many subordinate species are increasing (Appendix: Table A1). Furthermore, in dry meadows, the co-dominant *Selaginella densa* (Selaginellaceae) is decreasing, potentially allowing other subordinate species to increase (Appendix: Table A1). These changes suggest that species interactions might also vary over time along with variation due to topography, and that differential species responses will likely influence patterns of change in the tundra.

Conclusions

Our results suggest that considering the scale of environmental heterogeneity is critical to accurately understand responses to climate change in alpine and other topographically-complex environments. While we found some evidence of directional change with time, there is a primarily non-directional change over time where plots transition back and forth among community types in response to interannual variability. However, site-wide trends are showing that alpine tundra at Niwot Ridge is starting to respond directionally to changes in the environment. Site wide diversity is increasing (both taxonomic and functional) with some dominant species decreasing and shrubs and cushion plants increasing in abundance. We expect that these changes will likely continue to alter species composition, particularly as the directional change in mean environmental parameters surpasses interannual variability in these same parameters.

Acknowledgments

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Changes in individual species relative abundance (averaged across plots) across the tundra and within each community type. Only species that are significantly increasing (I) or decreasing (D) over time are shown. Negative slope values represent a negative relationship between a given species relative abundance and time and positive slope values indicate a positive relationship. *P < 0.05, **P < 0.01, ***P < 0.001.

Species	Slope	r^2	F	Functional group
Tundra wide				
Antennaria alpina	+0.006	0.77	21.74**	Forb
Artemisia scopulorum	+0.05	0.59	9.95*	Forb
Carex pyrenaica	+0.03	0.63	11.31*	Sedge
Chionophila jamesii	−0.01	0.52	7.57*	Forb
Clementsia rhodantha	+0.01	0.81	25.89**	Forb
Eremogone fendleri	+0.01	0.80	26.25**	Forb
Eritrichium aretioides	+0.003	0.50	6.95*	Forb
Gentiana algida	+0.006	0.70	14.75*	Forb
Geum rossii	−0.13	0.72	16.36**	Forb
Juncus drummondii	+0.05	0.84	32.67**	Sedge
Lloydia serotina	+0.06	0.78	22.09**	Forb
Luzula spicata ssp. *saximontana*	+0.02	0.90	52.89**	Sedge
Minuartia obtusiloba	+0.07	0.70	14.75*	Cushion
Pedicularis groenlandica	+0.001	0.55	8.43*	Forb
Potentilla diversifolia	+0.006	0.49	6.75*	Forb
Primula parryi	−0.03	0.68	13.61*	Forb
Rhodiola integrifolia	+0.002	0.55	8.26*	Forb

Table A1. Continued.

Species	Slope	r^2	F	Functional group
Salix glauca	+0.03	0.95	107.84**	Shrub
Salix planifolia	+0.01	0.85	35.32**	Shrub
Selaginella densa var. *scopulorum*	−0.09	0.71	15.53*	Forb
Sibbaldia procumbens	+0.06	0.56	8.60*	Forb
Trifolium dasyphyllum	+0.03	0.69	14.20*	N-fixer
Trisetum spicatum	+0.03	0.53	7.89*	Grass
Fellfield				
Artemisia scopulorum	+0.10	0.53	7.91*	Forb
Bistorta vivipara	+0.05	0.55	8.26*	Forb
Eremogone fendleri	+0.05	0.53	7.97*	Forb
Erigeron pinnatisectus	−0.02	0.53	7.86*	Forb
Eritrichium aretioides	+0.03	0.93	79.01**	Forb
Gentiana algida	+0.02	0.55	8.47*	Forb
Lloydia serotina	+0.26	0.81	28.07**	Forb
Saxifraga rhomboidea	−0.02	0.79	23.00**	Forb
Selaginella densa var. *scopulorum*	−0.34	0.80	25.72**	Forb
Dry meadow				
Campanula rotundifolia	+0.03	0.53	7.77*	Forb
Deschampsia caespitosa	+0.01	0.53	7.90*	Grass
Eremogone fendleri	+0.02	0.53	7.75*	Forb
Erigeron simplex	+0.03	0.60	10.14*	Forb
Hymenoxys acaulis	+0.02	0.56	8.77*	Forb
Lloydia serotina	+0.12	0.73	17.40**	Forb
Mertensia lanceolata	+0.01	0.68	14.02*	Forb
Salix glauca	+0.04	0.91	61.85**	Shrub
Selaginella densa var. *scopulorum*	−0.25	0.67	13.17*	Forb
Silene acaulis ssp. *subacaulescens*	+0.02	0.75	18.84**	Cushion
Trifolium dasyphyllum	+0.07	0.90	53.28**	N-fixer
Trifolium parryi ssp. *parryi*	+0.05	0.69	14.58*	N-fixer
Moist meadow				
Artemisia scopulorum	+0.10	0.73	17.73**	Forb
Chionophila jamesii	−0.02	0.68	13.70*	Forb
Gentiana algida	+0.04	0.67	13.34*	Forb
Geum rossii	−0.31	0.56	8.89*	Forb
Kobresia myosuroides	−0.06	0.49	6.72*	Sedge
Luzula spicata ssp. *saximontana*	+0.02	0.68	13.35*	Sedge
Minuartia obtusiloba	+0.06	0.65	12.24*	Cushion
Potentilla diversifolia	+0.01	0.63	11.03*	Forb
Rhodiola integrifolia	+0.01	0.53	7.88*	Forb
Stellaria longipes	+0.01	0.52	7.55*	Forb
Trisetum spicatum	+0.03	0.84	32.45**	Grass
Wet meadow				
Salix nivalis	+0.08	0.51	7.26*	Shrub
Snow bank–C				
Antennaria alpina	+0.07	0.72	16.77**	Forb
Caltha leptosepala	+0.90	0.67	12.99*	Forb
Carex pyrenaica	+0.33	0.55	8.21*	Sedge
Carex scopulorum var. *scopulorum*	+0.12	0.59	9.55*	Sedge
Clementsia rhodantha	+0.11	0.66	12.54*	Forb
Juncus drummondii	+0.66	0.53	7.81*	Sedge
Pedicularis groenlandica	+0.02	0.50	6.91*	Forb
Snow bank–S				
Carex lachenalii	+0.05	0.70	14.98*	Sedge
Carex scopulorum var. *scopulorum*	+0.03	0.79	23.79**	Sedge
Eremogone fendleri	+0.01	0.71	15.54*	Forb
Luzula spicata ssp. *saximontana*	+0.06	0.69	14.17*	Sedge
Minuartia obtusiloba	+0.15	0.56	8.71*	Cushion
Solidago spathulata var. *nana*	+0.01	0.69	14.69*	Forb
Trifolium parryi ssp. *parryi*	−0.29	0.57	9.09*	N-fixer