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RESEARCH ARTICLE

Divergent community trajectories with climate change across a fine-scale gradient in snow depth

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Abstract

1. Fine-scale microclimate variation due to complex topography can shape both current vegetation distributional patterns and how vegetation responds to changing climate. Topographic heterogeneity in mountains is hypothesized to mediate responses to regional climate change at the scale of metres. For alpine vegetation especially, the interplay between changing temperatures and topographically mediated variation in snow accumulation will determine the overall impact of climate change on vegetation dynamics.
2. We combined 30 years of co-located measurements of temperature, snow and alpine plant community composition in Colorado, USA, to investigate vegetation community trajectories across a snow depth gradient.
3. Our analysis of long-term trends in plant community composition revealed notable directional change in the alpine vegetation with warming temperatures. Furthermore, community trajectories are divergent across the snow depth gradient, with exposed parts of the landscape that experience little snow accumulation shifting towards stress-tolerant, cold- and drought-adapted communities, while snowier areas shifted towards more warm-adapted communities.
4. *Synthesis*: Our findings demonstrate that fine-scale topography can mediate both the magnitude and direction of vegetation responses to climate change. We documented notable shifts in plant community composition over a 30-year period even though alpine vegetation is known for slow dynamics that often lag behind environmental change. These results suggest that the processes driving alpine plant population and community dynamics at this site are strong and highly heterogeneous across the complex topography that is characteristic of high-elevation mountain systems.

KEYWORDS
alpine vegetation, climate change, community trajectories, snow gradients, topography

1 | INTRODUCTION

Topography, especially in mountainous areas, has large impacts on the distributions of species (Scherrer & Körner, 2011), communities (Isard, 1986), functional traits (Spasojevic & Suding, 2012) and ecosystem-level processes (Fan et al., 2016), resulting in a mosaic of vegetation types across topographically complex landscapes. Variation in abiotic and biotic conditions across topographic gradients may also shape how vegetation within a single landscape responds to regional climate change (Ackerly et al., 2020; Elsen & Tingley, 2015). Local shifts in species distributions across mesotopographic gradients (0.01–1 km; e.g. impacts of slope, aspect and relative elevation), rather than large-scale shifts in latitude or elevation, may be one of the earliest biogeographic responses by species to climate change (Antão et al., 2022; Rapacciuolo et al., 2014). However, as this local topography can jointly impact population, community and evolutionary dynamics, there are many potential scenarios for how the mosaic of vegetation may respond, both in magnitude and direction, to changing climate (Graae et al., 2018). Communities' responses across topographically complex landscapes may vary due to the extent to which they are exposed to changing climate (Dickinson et al., 2015), including by shifts in the dominant climate variable impacting the vegetation (e.g. temperature and moisture; Oldfather et al., 2020), the climate sensitivities and responsiveness of constituent species (Kulonen et al., 2018) and the importance of climate-mediated community interactions (Alexander et al., 2015; Collins et al., 2022).

No ecosystem better demonstrates the critical role of local topography than alpine tundra, where composition can completely turn over and biomass can vary 10-fold over a span of metres (Spasojevic & Suding, 2012). Additionally, there has been rapid warming at high elevations (Pepin et al., 2015) and alpine plants are sensitive to changing temperature physiologically (Körner, 2021b), demographically (Doak & Morris, 2010; Oldfather et al., 2021) and ecologically through shifting community interactions (Alexander et al., 2015). Broad-scale analyses of alpine responses to climate change show an increase in species richness due to encroachment of low-elevation species, lagged extinctions of high-elevation species and increases in the abundances of warmer-adapted species (i.e. thermophilization; Pauli et al., 2012; Rumpf et al., 2018; Steinbauer et al., 2018). However, topographic heterogeneity of alpine areas may lead to divergent responses to regional climate change at the scale of metres that are on par with the differences observed in species responses at much larger spatial and temporal extents (Oldfather et al., 2021; Sandvik & Odland, 2014; Scherrer & Körner, 2011; Suggitt et al., 2018).

Understanding the interplay between changing temperatures and topographically mediated variation in snow accumulation is expected to be crucial for predicting the overall impact of climate change on vegetation dynamics in alpine systems (Niittynen, Heikkinen, & Luoto, 2020). Snow provides insulation during the winter, supplies moisture as it melts in spring and constrains the length of the growing season—all of which are important for alpine plants (Rixen et al., 2022). Mean annual snowfall in the western contiguous United States has decreased over the last 70 years (Mote et al., 2018), though local patterns are highly variable across space. The combined impacts of topography, shrubs and wind can drive consistent patterns of fine-scale spatial variation in snow persistence and depth across alpine landscapes (Litaor et al., 2008), although this may change with future snow loss (Badger et al., 2021). Importantly, gradients in snow mediate the climate drivers that control alpine vegetation dynamics (Fan et al., 2016). Energy limitation is predicted to be the major factor in vegetation dynamics in snowier sites with shorter growing (snow-free) seasons, while soil moisture is the limiting factor in wind-exposed areas that receive little water from melting snow (Fan et al., 2016). Landscape positions with reduced snowpack may also experience harsher wintertime conditions due to increased exposure to freezing temperatures and damaging wind when snow is thin (Niittynen, Heikkinen, Aalto, et al., 2020). Consequently, we might expect that rising temperatures will relax energy limitation in snowier sites leading to longer, warmer growing seasons, while exacerbating water limitation and freezing exposure in areas that accumulate little or no snowpack during the winter (Dolezal et al., 2020).

Topographically mediated snow gradients may also impact the direction of local community responses to warming. Interspecific variation in climate responses reflects differences in the unique physiological, developmental and morphological traits that have evolved in each lineage in response to past climates (Carscadden et al., 2020; Jackson et al., 2009; Nadeau et al., 2017). As a result, measurements that capture species' adaptations to past climate can serve as useful predictors of species-level responses to current and future climate change. Recent studies have demonstrated that incorporating climate niche information, typically estimated as the climate conditions encompassed within a species geographic range, can help explain different temperature responses among species within communities (Lynn et al., 2021), biomes (Blonder et al., 2015) and geographic regions (Peng et al., 2021). Functional traits may also predict species responses to climate change (Bjorkman et al., 2018): Species with resource-acquisitive traits (i.e. traits that allow them to rapidly acquire and process resources) often respond faster to environmental change than species with more conservative resource use strategies (Soudzilovskaia et al., 2013).

Long-term data provide a powerful tool for measuring the effects of climate change on vegetation (Elmendorf et al., 2015), but datasets that explicitly capture plant responses across fine-scale topographic gradients are few and far between. Here, we harnessed the power of a long-term monitoring program of temperature, snow and plant community composition in a mountain ecosystem at the Niwot Ridge Long Term Ecological Research site (NWT LTER) in Colorado, USA, to explore alpine vegetation community trajectories across a snow depth gradient (Figure S1). Previous work at NWT LTER found limited site-level directional community change in the alpine tundra vegetation from the 1970s to the early 2000s, potentially due to fine-scale topographic heterogeneity (Bueno de

Mesquita et al., 2018; Scharnagl et al., 2019; Spasojevic et al., 2013). We build on this work by interrogating the patterns of community change across a spatial gradient in snow depth, including an additional decade of community composition and climate data, and explicitly linking compositional turnover with changes in functional and thermal niche traits. In topographically complex landscapes like the alpine tundra, capturing community change at fine spatial scales is key to quantifying the biological effects of changing climate. We hypothesize that the response of the alpine vegetation to changing climate will be dependent on fine-scale gradients of snow depth. First, we predict that plant communities in microsites at the extremes of the snow depth gradient will respond to warmer temperatures, with communities in snowier sites experiencing an increase in growing season length and less snowy sites experiencing exacerbated soil moisture limitation. Second, we predict that warming will favour an increase in warm-adapted, acquisitive species in relatively snowy sites, while communities in areas with less snow accumulation will shift towards more conservative, drought-adapted species, not necessarily associated with warmer thermal niches.

2 | MATERIALS AND METHODS

2.1 | Vegetation survey description

The NWT LTER site (40°03′ N, 105°35′ W, 3528 m. a.s.l.) is located in the Southern Rocky Mountains, and scientists have studied the responses of the mountain ecosystem to changing environmental conditions at this location for over 40 years. The NWT LTER saddle vegetation dataset consists of community composition records from 88 1 m × 1 m plots arranged in a grid in the alpine tundra at Niwot Ridge (Walker, Humphries, & Niwot Ridge, 2022; Figure S1). Plots are located in the 'saddle', a 7000 m^2 area that runs east–west between two knolls, and span plant community types that range from snowbed communities with relatively deep, persistent snowpack that does not melt until mid-summer, to windswept fellfield communities that are rarely snow-covered, even during the winter (Spasojevic et al., 2013). This site was grazed by sheep in the 1940s, but there has been no domestic grazing at this site since that time (Formica et al., 2014). Plant community frequency surveys were conducted for 2 consecutive years, then approximately every 5 years from 1989 to 2010 and then again on an annual basis from 2010 to the present (1989, 1990, 1995, 1997, 2006, 2008 and 2010–2020; Walker, Humphries, et al., 2022). The identification of the species present was recorded at 100 evenly spaced points within the plot (point-intercept method). In earlier surveys, only the top plant intercepted at each point was recorded ('top hits'). More recently, multiple hits were recorded per point measurement if different species came into contact with the point measurement. Only top hits were used for all analyses in this study to standardize the method of data collection over time. All fieldwork performed to collect the vegetation (and climate) data was permitted through the CU Boulder Mountain Research Station.

2.2 | Climate data

Temperature has been recorded daily by electronic data logger since 1986 at a single meteorological station adjacent to the saddle vegetation plots (White et al., 2023). Quality control and infilling methods used 24 weather stations at NWT LTER or elsewhere in the region for comparison with the saddle record. After QC and gap-filling, data were homogenized to account for four instrument changes over the electronic record by adjusting temperature data to the most recent instrument at the saddle station. For adjustments, we used a 1-year overlap period between the outgoing and incumbent saddle temperature electronic instruments, as well as each instrument's average relationship to a nearby, independently maintained, quality-controlled, gap-filled record spanning the entire period of instrument changes (Blanken et al., 2016).

At each of the 88 plots, measurements of snow depth were taken 1–2 times a month from February to July since 1990 (Walker, Morse, et al., 2022). May snow depth averaged across all time points was used as the metric for plot-level snow depth, since plots with more spring snowpack remain snow-covered for longer periods of time. In 1 year (2008) when no measurements were taken in May, the snow survey data from the last date in April (04-29-2008) were used. The snow depth of each plot was averaged across all snow survey years to calculate the mean snow depth of each plot, and plots were then divided into 'low snow', 'average snow' and 'high snow' categories, hereafter referred to as LS, AS and HS, respectively, reflecting the temporal consistency of spatial patterns of the snow gradients at this site (Litaor et al., 2008). Plots were binned into snow depth categories in order to more clearly visualize and interpret known nonlinear responses of community change across the snow depth gradient. We chose three categories to balance equal and sufficient plot replication within each group with the loss of statistical power due to binning. Snowpack variation (plot-level variation in mean May snowpack across the study period) within each category ranged from 4 to 42 cm in LS plots, 42–198 cm in AS plots and 203–351 cm in HS plots.

2.3 | Metrics of plant community change

Community turnover was calculated as a multivariate metric summarized across plots using the *multivariate_change* function from the Codyn package (Hallett et al., 2016) in R (R Core Team, 2022). This approach quantifies the dissimilarity (Bray–Curtis) between the composition of communities over time by calculating the distance in ordination space (using PCoA ordination axis 1 and 2) between the centroids of the plot replicates in each time point relative to the centroid of the plots in the 1990 survey (Figure S5). The dispersion of each group (i.e. each snow category) through time was calculated as the distance between all plots and the group centroid for each time point (Figure S5). The first two PCoA axes explained 47% of the community variation for HS plots, 46% for AS plots and 66% for LS plots. We applied linear mixed effects models to test for temporal trends in the compositional turnover with year, snow depth category and the interaction between year and snow depth as predictors and included year as a random effect.

To assess whether the representation of 'warm-adapted' species has increased (thermophilization) or decreased (reverse thermophilization) over time in these alpine plant communities, we calculated the climate niche value for each plant species that was documented in the community surveys. We used Google Earth Engine (Gorelick et al., 2017) to extract annual average temperatures for all Global Biodiversity Information Facility (GBIF) locations of the constituent species (Oldfather, 2022) from the TerraClimate dataset (Abatzoglou et al., 2018). Prior to climate extraction, duplicate GBIF records, as well as those found to be at sea or near biodiversity institutions, were removed with the CoordinateCleaner package in R (Zizka et al., 2019). The extracted climate values were averaged to get species-specific climate niche values. Niche values assessed from North American species distributions were comparable to values that were calculated when species locations were restricted to the Southern Rockies Ecoregion (Omernik & Griffith, 2014), so results presented here are based on the species North America distributions. We calculated the abundance-weighted mean climate niche for each plot in each sampling year to obtain a spatially replicated time series of community-weighted thermal niche (CWTN) values. Linear mixed effects models were used to test for temporal trends in the CWTN with year, snow depth category, the interaction between year and snow depth, and random effects of year and plot.

NWT LTER maintains a functional trait database (Spasojevic & Weber, 2021; Spasojevic et al., 2022) that has trait data for 84.4% of species that have been found in the saddle plots and identified to species level and these species make up between 75% and 98% of the total cover across the 88 plots we sampled, depending on the trait. NWT-wide averages of the functional traits for each species were used in this analysis. We focussed on a subset of the field-measured functional traits that were well-sampled for the constituent species: height, leaf dry matter content, water-use efficiency (WUE), as described by the proxy δ13C isotopes which represents the balance between photosynthetic capacity and water loss (Spasojevic & Weber, 2021), and specific leaf area. The resulting community-weighted mean trait coverage was high across all selected traits (per cent coverage of hits for each plot with corresponding data for plant height: 98%[mean], 78%[min]; specific leaf area 98%[mean], 78%[min]; leaf dry matter content: 97%[mean], 75%[min]; water-use efficiency: 96%[mean], 75%[min]). The abundance-weighted mean for each functional trait was calculated for each plot at each time point to get a spatially replicated time series of community functional trait values. Linear mixed effects models were used to test for temporal trends in the community-weighted functional traits (CWFT) with the response variable of CWFT, predictor variables of year, the snow depth group (factors), the interaction between year and snow depth group, and random effects of year and plot. A separate mixed effects model was built for each of the four functional traits.

2.4 | Species-specific responses

The relationships between local (plot-level) species losses, gains and changes in abundance were examined for all species to investigate the species-level responses driving the community trends. Species losses were defined as a species being present in at least one of the first two original surveys and not being present in either of the final two surveys. Species gains were quantified as a species being absent in at least one of the first two original surveys and present in either of the final two surveys. We approached species losses and gains in this manner to be conservative in estimating local colonization and extinction from point-intercept frequency data, where rare species are likely to be mistakenly characterized as absent if they are missed in a single survey. Change in abundance was quantified for each species as the slope of species-specific abundance regressed across years and plots within each snow group.

Generalized linear mixed effects models were used to test for interactions between the thermal niche of the constituent species and snow depth in predicting the likelihood of species gain (binomial error structure), species loss (binomial error structure) and change in abundance (Gaussian error structure). The models for these three response variables included year, snow depth group (factors), the interaction between year and snow depth group as predictor variables, and random intercepts for species and plot. We also analysed change in abundance using a Theil-Sen estimator to confirm that the results of the linear model were not driven by the leverage of two species that had relatively large changes in abundance through time. These results of the linear and Theil Sen estimator models were qualitatively similar, so only results from the linear model are presented.

All statistical analyses for both the community and species-level trends were analysed in R 4.2.1 (R Core Team, 2022). All generalized mixed models were performed using the R lme4 package (Bates et al., 2015). For all metrics, the marginal linear means (least-squares means) of the temporal trends for each of the snow depth groups were calculated using the *emtrends* function in the R emmeans package (Lenth, 2022). In calculating confidence intervals, the Tukey adjustment was used to adjust for multiple comparisons.

3 | RESULTS

3.1 | Changing climate

We found that temperatures at Niwot Ridge have increased over the last four decades, particularly during summer (Figure 1), leading to a strong increase in the cumulative temperature experienced by the alpine vegetation during the growing season (growing degree-days; Figure S2). In contrast, snow records from across all saddle plots and other measurements of snow depth and precipitation at Niwot Ridge are highly variable through time and do not show any detectable landscape-level directional change in snowpack to date (Figures S3 and S4A). Within the snow depth groups, areas on the landscape with the highest snowpack show a slight trend in decreasing springtime (slope and 95% confidence intervals for LS: 0.099 (−2.09–2.288), AS: 0.052 (−2.14–2.243), HS: −2.582 (−4.77 to −0.391; Figure S4B) and wintertime snowpack (slope and 95% confidence intervals for LS: 0.099 (−2.09–2.29), AS: 0.052 (−2.14–2.24); HS: −2.58 (−4.77 to −0.39)).

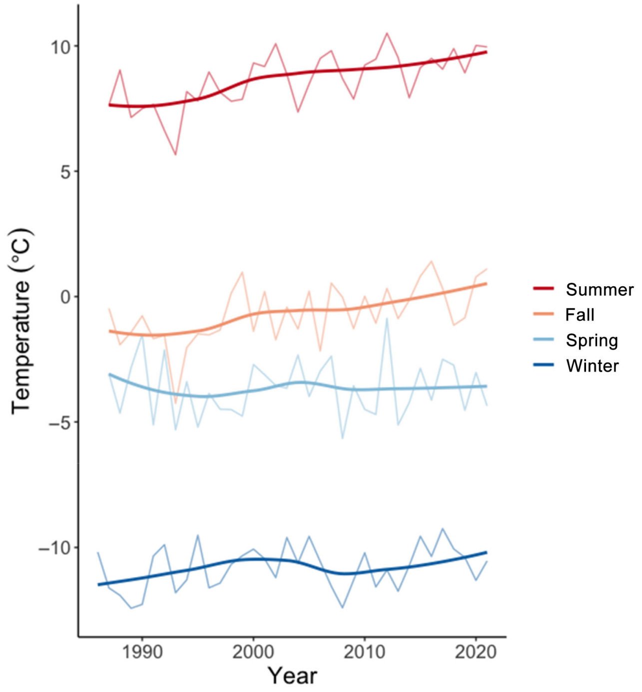

FIGURE 1 Temporal trends in mean annual temperature by season from a meteorological station adjacent to the saddle community plots on Niwot Ridge (Morse et al., 2022; Morse & Losleben, 2019). Thin lines represent annual variability, and thick lines represent LOESS fit through time.

3.2 | Community turnover through time

Our analyses of long-term trends in plant community composition for each snow category reveal striking patterns of directional change in the alpine vegetation at Niwot Ridge since 1990. Although there has been significant compositional change in all three snow categories, communities at the extremes of the snow depth gradient (LS, HS) showed the largest changes (Figure 2a). Low snow plots have shown the greatest magnitude of change through time, followed by the snowy and average snow plots (slope and 95% confidence intervals of annual per cent change in community composition for LS: 0.006 (0.005–0.007), AS: 0.004 (0.002–0.005), HS: 0.005 (0.004–0.007)). The high snow plots have also increased in mean plot richness (alpha diversity) through time, while average and low snow plots have remained unchanged in terms of richness (Figure S6, slope and 95% confidence intervals for LS: 0.005 (−0.029–0.018), AS: 0.005 (−0.02–0.029); HS: 0.07 (0.046–0.094). Furthermore, high snow sites have converged towards more similar community composition (reduced dispersion and lower beta diversity), while low and average snow sites have become more heterogeneous (increased dispersion and higher beta diversity; Figure 2b).

3.3 | Thermophilization and functional trait shifts

The community-weighted temperature affinities and functional traits of the alpine community have also significantly shifted through time (Figure 3). Interestingly, these shifts are in different directions depending on snow depth: High snow plots have shifted towards more warm-adapted species (thermophilization), while the most exposed sites have experienced an increase in cool-adapted species

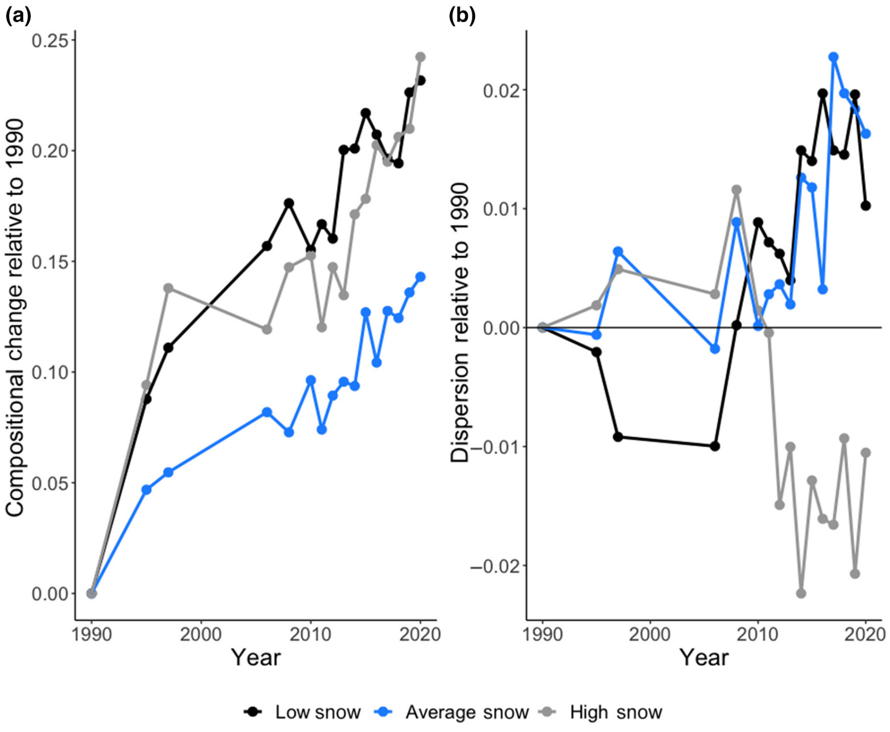

FIGURE 2 (a) Magnitude of compositional change through time relative to the vegetation communities in 1990 for the three snow depth groups. Points for each time point represent the shift in the centroid of all plots in ordinations space. A relative compositional change value of 0.25 indicates a 25% shift through time. (b) Beta diversity (dispersion) through time relative to the beta diversity in 1990 across the snow depth groups.

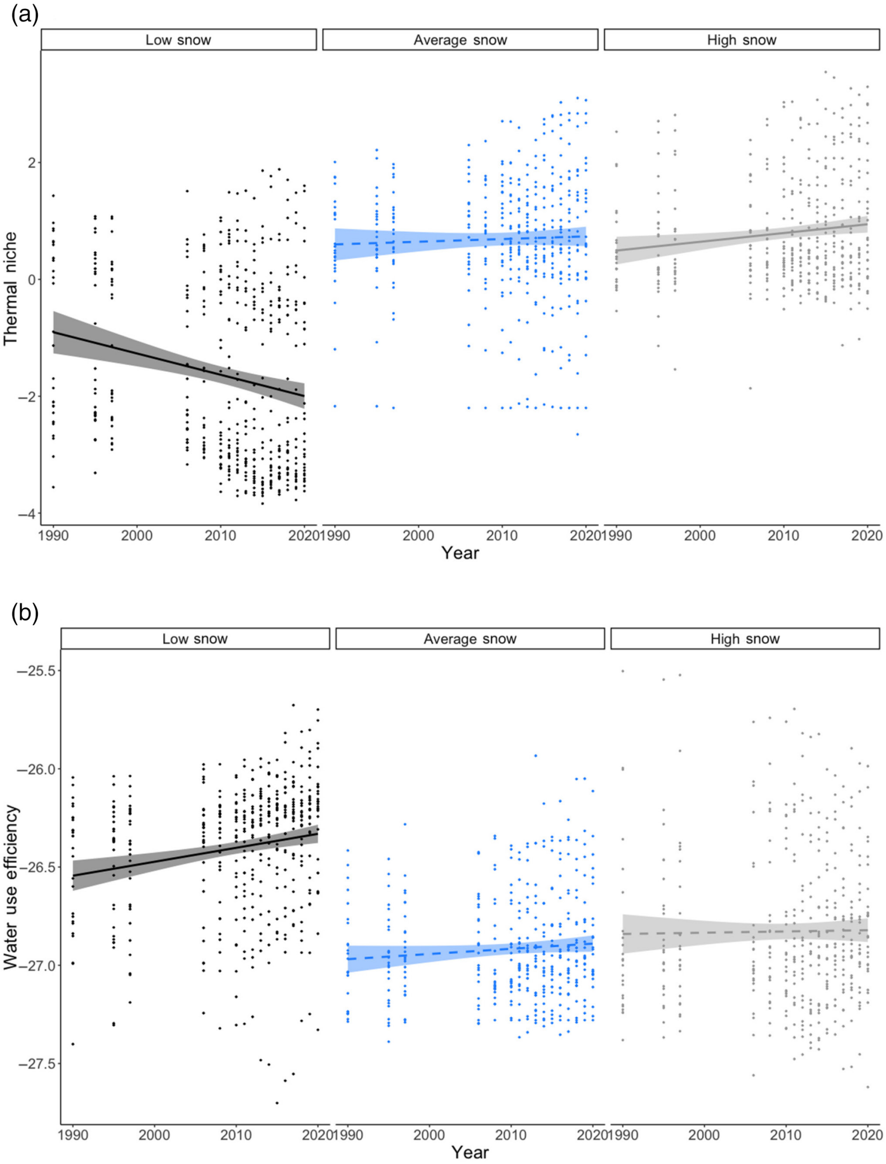

FIGURE 3 Community-weighted (a) mean annual temperature niche (°C) and (b) water-use efficiency values (WUE; Δ δ13C) through time for the three snow depth groups. Points indicate a community-weighted mean for each plot in each time point. Dashed lines indicate nonsignificant trends ($p > 0.05$) through time; solid lines indicate significant trends through time. 95% confidence intervals based on ordinary least-squares linear regression are shown as shaded areas around the trend lines.

(Figure 3a, slope and 95% confidence interval for LS: −0.036 (−0.041 to −0.032), AS: 0.004 (−0.001–0.009); HS: 0.015 (0.01–0.02)). Height (Figure S7A, slope and 95% confidence intervals for LS: 0.047 (0.015–0.08), AS: 0.148 (0.115–0.182); HS: 0.096 (0.062–0.129) and leaf dry matter content has increased across the whole landscape (Figure S7B, trend and 95% confidence intervals for LS: 0.516 (0.264–0.767), AS: 0.631 (0.375–0.887, HS: 0.806 (0.551–1.062)). Specific leaf area (SLA) has significantly declined across the landscape, with a stronger trend in high snow depth plots (Figure S7C, slope and 95% confidence intervals for LS: −0.106 (−0.178 to −0.034), AS: −0.135 (−0.211 to −0.059), HS: −0.371 (−0.447 to −0.296)). In average and high snow sites, water-use efficiency did not change through time (Figure 3b, slope and confidence intervals for AS: 0.001 (−0.0002–0.002), HS: 0.0003 (−0.001–0.002)) but significantly increased in low snow sites (Figure 3b, trend and 95% confidence intervals for LS: 0.007 (0.006–0.009)). Furthermore, there was a weak (nonsignificant) negative correlation between the thermal niche and water-use efficiency traits of the constituent species (Figure S8).

3.4 | Species-specific responses

Overall, low snow sites had higher rates of species losses (average species losses across the study period for LS = 0.322, AS = 0.251, HS = 0.258) and species gains (average species gains across the study period for LS = 0.046, AS = 0.029, HW = 0.040) through time (higher temporal turnover) relative to average and high snow sites. These rates of species losses and gains are meaningful in terms of the overall low plot-level richness of this system, with the average richness of 11 species in low snow plots and 9 species in average and high snow plots. However, species' thermal niches were not predictive of species losses (group estimates and asymptotic 95% confidence intervals of the effect of the thermal niche on the probability of local species losses for LS: 0.069 (−0.120–0.258), AS: −0.19 (−0.433–0.054), HS: −0.177 (−0.465–0.111)) and gains (group estimates and asymptotic 95% confidence intervals of the effect of the thermal niche on probability of local colonization for LS: −0.017 (−0.184–0.151), AS: 0.016 (−0.162–0.193), HS: −0.056

(−0.229–0.116)). In contrast, we observed a significant negative relationship between species' thermal niche and changes in abundance in low snow areas through time (Figure S9; trend and 95% confidence intervals for LS: −1.121 (−1.872 to −0.369), AS: 0.506 (−0.397–1.408, HS: 0.738 (−0.301–1.776)) indicating the importance of species-specific changes in cover for the observed thermophilization and reverse thermophilization patterns. Two graminoids (*Deschampsia cespitosa* (L.) Beauv. and *Kobresia myosuroides* (Vill.) Fiori & Paol) stand out as having an approximate fourfold higher increase in abundance relative to other species across the snow depth gradient. The more stress-tolerant perennial sedge *K. myosuroides* is most abundant in exposed sites (Theodose & Bowman, 1997a) and has substantially increased through time in these low snow areas (Figure 4a). The more acquisitive perennial grass *D. cespitosa* has increased across the whole landscape, but the rate of increase is significantly higher in snowier sites (Figure 4b).

4 | DISCUSSION

The large and divergent community shifts with the last 30 years of warming at both extremes of the snow depth gradient are consistent with the expectation that the limiting conditions that control alpine vegetation dynamics are mediated by patterns of snow depth across the terrain—with moisture limitation driving plant responses in low snow locations while constraints on the length of the growing season control responses in snow persistent locations. With summertime warming, exacerbation of moisture limitation through drying could likely have driven the large, but spatially diverse, compositional shifts in the exposed sites. In high snow sites, the high compositional turnover is potentially due to the joint changes of increasing temperature and decreasing snowpack experienced by the vegetation in these plots. However, species composition in this environment is also spatially homogenized, as illustrated by the decreased dispersion. This indicates that the direct impacts of temperature on the energy availability of these systems have a more spatially consistent impact on community composition. The muted turnover in the average snow sites may be due to species within these communities responding to concurrent changes in energy and water availability. If the dynamics of these two limiting drivers push the average snow communities in different directions, their ability to respond to climate change may be limited (Oldfather et al., 2020) or lead to novel communities (Ordonez et al., 2016).

The thermal and functional traits of the alpine plant communities at Niwot Ridge have also shifted through time and, in many cases, exhibited divergent patterns across the snow depth gradient. The thermophilization shift in high snow sites matched our predictions, although it is a weak trend. However, in direct contrast to our predictions of minimal shifts in the thermal niche of the low snow community, we saw a strong pattern of 'reverse thermophilization'

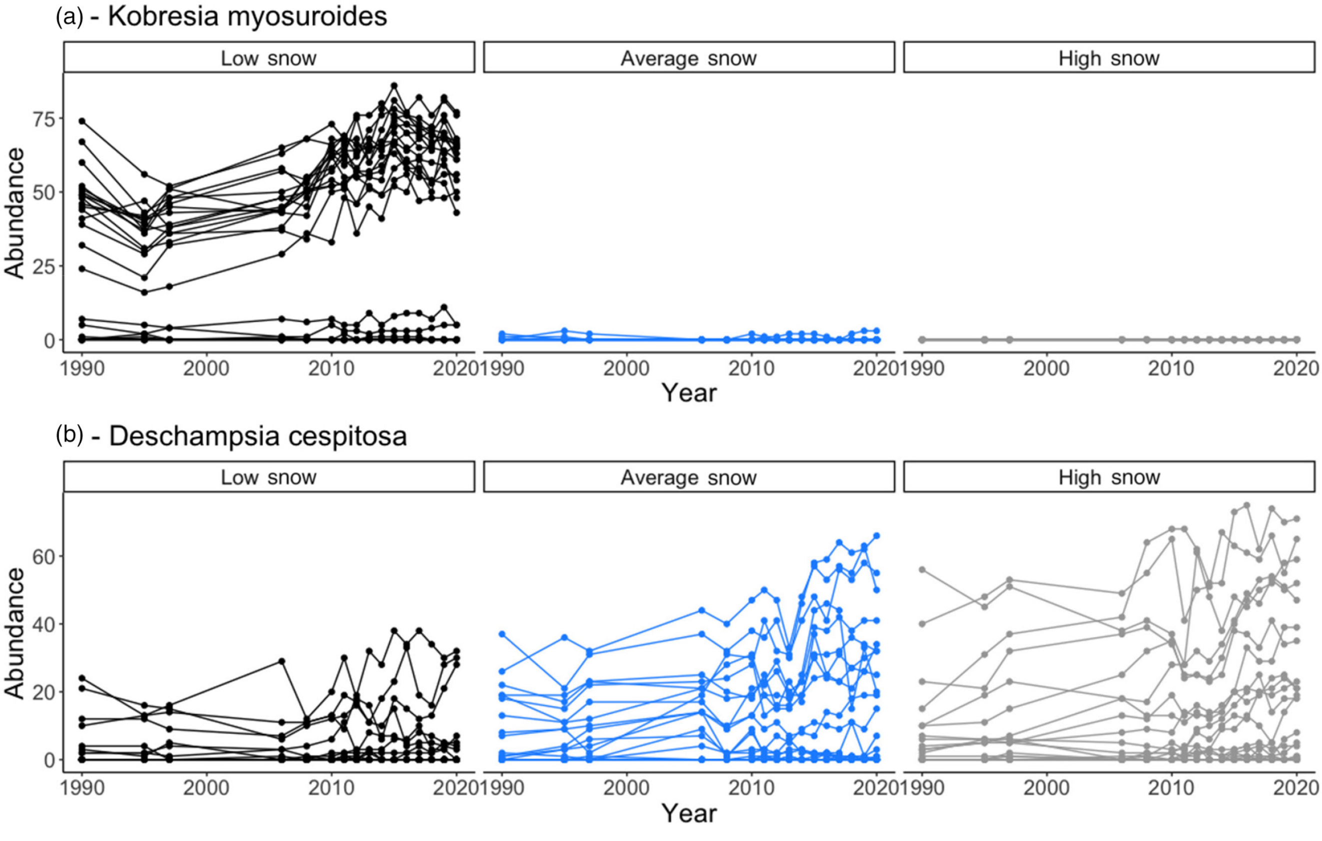

FIGURE 4 Abundance (number of hits) of the two dominant species across the saddle plots (a) *Kobresia myosuroides* and (b) *Deschampsia cespitosa* through time within each snow depth group. Points represent plot-level measurements at each time point.

in the more exposed sites. We posit that this pattern may be due to the association between cold and drought tolerance (Pescador et al., 2016; Sierra-Almeida et al., 2016) as the physiological mechanisms (e.g. osmotic regulation) for freezing tolerance also promote drought tolerance (Körner, 2021a; Pescador et al., 2016). Therefore, the observed reverse thermophilization may in fact be a shift to more drought-tolerant species in the low snow communities. The reverse thermophilization pattern may also be shaped by increasing exposure to wintertime cold temperatures (Niittynen, Heikkinen, Aalto, et al., 2020). However, the snow data indicate that wintertime (December–February) snow depth has not changed through time except for a slight decrease in the snowiest plots. With the exception of the increase in plant height, which is associated with resource-acquisitive strategies, the shifts in functional traits that we detected at Niwot Ridge align with broad trends of alpine plant communities across the Rocky Mountains that have shifted towards more conservative, stress-tolerant traits (Huxley & Spasojevic, 2021). However, we observed that different traits drove this conservative shift across different parts of the landscape—increased water-use efficiency in exposed sites and decreased SLA in snowier sites—indicating divergent trajectories of the communities across the snow depth gradient.

Community-level changes in thermal and functional traits can be driven by multiple patterns of response at the species level: colonization and/or extinctions of species, relationships between shifts in abundance of multiple constituent species and trait values, and large changes in a dominant species with an extreme trait value. We found evidence for the latter two drivers only, and their relative impact differed across the snow depth gradient. Our findings indicate that community-level shifts in the alpine vegetation at Niwot Ridge are driven by changes in the abundance of resident species over the past 30 years, especially in areas with little snowpack, rather than by species turnover through colonization and extinction events. While our sampling may have missed colonizations or extinctions of rare species, support for shifts in abundance, rather than species turnover, as a mechanism of thermal and functional change is consistent with the slow-growing, high survivorship that is characteristic of alpine plant demography (Körner, 2021a). Our findings highlight the lags in dispersal and demography inherent in alpine plant communities despite the proximity of the study plots to each other, which could facilitate fine-scale range shifts by dispersal across the heterogeneous terrain (Alexander et al., 2018). Therefore, even over 30 years, the impact of warmer conditions has not yet caused measurable patterns of local population extinction or colonization.

The two species that showed the largest increases in abundance (*K. myosuroides* in less snowy sites and *D. cespitosa* in snowier sites) are the dominant graminoids in the alpine plant community at Niwot Ridge and, as a result, their ecology has been thoroughly studied. While we cannot eliminate the possibility that the long-term trends of these two species reflect their ongoing response to a release from grazing pressure that ended in the 1940s (Formica et al., 2014), their responses are also consistent with our understanding of their associations with temperature and moisture gradients at Niwot Ridge. Specifically, *D. cespitosa* is often associated with wetter landscape positions and its warm thermal niche may be the primary driver of the community-level thermophilization trends in high snow plots. Although multiple species are likely driving the reverse thermophilization patterns observed in low snow sites, as indicated by the significant negative relationship between the thermal niche and abundance change, *K. myosuroides*' relatively cool thermal niche value is likely a large contributor to this community-level pattern. Furthermore, it has been established that *K. myosuroides* is limited to low snow areas due to an inability to cope with the shortened growing season of snowier locations (Bell & Bliss, 1979). In contrast, *D. cespitosa* is out-competed in less snowy sites by *K. myosuroides*, which can form tussocks that increase intraspecific soil moisture availability while limiting the soil moisture available to other species (Theodose & Bowman, 1997b). The ability of *K. myosuroides* to form mats that exclude other species may further contribute to lags in the community turnover in response to warming conditions.

In conclusion, our long-term analysis of climate and vegetation at Niwot Ridge reveals that fine-scale heterogeneity in snow accumulation and depth can drive divergent community trajectories in response to climate change within a single landscape. Wind-blown areas of the landscape have shifted towards stress-tolerant, cold- and drought-adapted communities, while snowier locations shifted towards more warm-adapted communities. Furthermore, our findings indicate that both the direct effects of temperature and the indirect effects of soil moisture are likely driving this dynamic. Although patterns of reverse thermophilization in exposed sites have also been posited to be due to reductions in snowpack leading to exposure to colder springtime temperatures (Körner, 2021a; Šímová et al., 2017), our joint exploration of the temporal patterns in temperature, snow and thermal and functional niche traits of the vegetation do not support this hypothesis. Rather, the magnitude of community shifts in both extremes of the snowpack gradient, lack of change in snowpack through time for low snow areas, increase in the community's water-use efficiency and increase in *K. myosuroides* abundance collectively support the hypothesis that community responses to rising temperature in low snow areas are driven by increasing moisture limitation. Divergent community trajectories across moisture gradients align with temporal trends observed at much broader spatial scales: for example, moist boreal-temperate mountain peaks exhibit patterns of invasions of warm-adapted low-elevation species that are not observed in the moisture-limited Mediterranean mountains (Pauli et al., 2012). Lastly, our study system is known for slow change and lagging demographic responses, underscoring the strength of the processes driving these divergent shifts across the landscape (Nomoto & Alexander, 2021).

Mountainous regions represent 10% of the Earth's land surface, support a third of terrestrial species diversity and supply water to half of the global human population (Immerzeel et al., 2020). Our results indicate that climate change is exacerbating the differences in topographically structured alpine vegetation in these mountain landscapes, leading to landscape-scale biotic differentiation. As a result, the types of species that will be successful or decline in the face of a changing climate can change over the scale of metres. We expect that this phenomenon is not limited to alpine ecosystems. For example, there is a high degree of microclimate variation both within forests (Zellweger et al., 2020) and urban ecosystems (Schwaab et al., 2021), where overstory tree cover can play an analogous role to alpine snow cover in buffering climate exposure of understory plants. Furthermore, divergent community responses may exacerbate fine-scale biotic and climatic gradients, potentially promoting the resilience of the overall landscape by increasing genetic, population and community diversity through time (Lawler et al., 2015). This interpretation contrasts with concerns that climate change may lead to biotically homogenized landscapes, reducing the ability of the system to respond to further change (Gao et al., 2019; Walter et al., 2021). However, if we extend this logic to alpine community types within a landscape, we expect future high snow areas, which are becoming more homogenous, to be less resilient than low snow areas, which are becoming more heterogeneous. Future community trajectories hinge on future snowpack patterns, which are generally declining in the mountains across the western contiguous United States (Musselman et al., 2021). As winter snowfall continues to decline and snowmelt occurs earlier in the season, the current community trajectories will likely change as water limitation becomes a more dominant driver in currently snowy parts of the landscape (Dolezal et al., 2020). If so, this biotic divergence due to the snow depth gradients could be a short-term response of the landscape to a warming climate and lead to communities in snowier parts of the landscapes to be less able to cope with future drier conditions.

AUTHOR CONTRIBUTIONS

Meagan F. Oldfather and Nancy C. Emery conceived of the study. Meagan F. Oldfather led the analyses and writing of this manuscript. Sarah C. Elmendorf, Caitlin T. White, Jonathon J. Henn, Jared D. Huxley, Elsa Van Cleemput and Hope C. Humphries contributed to the analyses and writing. Marko J. Spasojevic, Katharine N. Suding and Nancy C. Emery contributed to the writing. Hope C. Humphries and Marko J. Spasojevic collected the majority of the data.

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CONFLICT OF INTEREST STATEMENT

Johnathan Henn is an Associate Editor of Journal of Ecology, but took no part in the peer review and decision-making processes for this paper.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14223.

DATA AVAILABILITY STATEMENT

All temperature, precipitation and vegetation data used in this study are publicly available on the NWT LTER data catalogue (https://nwt.lternet.edu/data-catalog) and archived by the Environmental Data Initiative. Specific data products are cited throughout the manuscript and direct links to all data are as follows: https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-nwt.78.3; https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-nwt.405.6; https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-nwt.500.3; https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-nwt.93.6; https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-nwt.31.19; https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-nwt.314.1; https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-nwt.186.3; https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-nwt.294.1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Map of gridded plots (black dots) at Niwot Ridge Long Term Ecological Research site (NWT LTER) in Colorado, USA, overlayed on a backdrop of modeled average day-of-year (DOY) of snow melt-out from 1996 to 2019 (30 m resolution, resampled to 1 m resolution; Yang et al., 2021).

Figure S2. Growing degree-days (summation of average daily temperature for days where the average daily temperature is greater than 0°C) through time based on saddle temperature data (White et al., 2023).

Figure S3. Temporal trends in total annual precipitation by season from the D1 meteorological station (3738 m) on Niwot Ridge (Kittel et al., 2021).

Figure S4. (A) Annual average May snow depth (cm) across the entire landscape shows no significant trend through time (Estimate = 0.8005, p-value = 0.455). (B) Annual average May snow depth (cm) through time for each snow persistence group time. Dashed lines indicate non-significant trends ($p > 0.05$) through time; solid lines indicate significant trends through time.

Figure S5. PCoA ordination of the communities in the three snow persistence groups in 1990, 2010, and 2020.

Figure S6. Model fits of mean plot richness trends through time by snow persistence group.

Figure S7. Community-weighted height (A) and leaf dry matter content (LDMC) (B) and specific leaf area (SLA) (C) values through time for the three snow persistence groups.

Figure S8. Correlations between all focal functional and thermal niche traits.

Figure S9. Relationships between the thermal niche and temporal changes in abundance by snow persistence group.

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