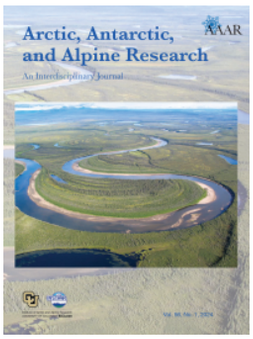

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Shifting alpine plant distributions with global change: Testing the environmental matching hypothesis

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ABSTRACT

Species facing novel temperature, precipitation, and nitrogen (N) deposition regimes must move or adapt to persist. For long-lived plants, a primary form of climate acclimation is through shifting geographic range limits or establishing in favorable microclimates. One commonly assumed but rarely tested hypothesis is that these shifts can be predicted by environmental matching: that the environmental characteristics that define a current distribution should predict how a population will shift with environmental changes. To test this hypothesis, we transplanted four alpine and two subalpine plant species into environments with experimentally increased temperature, snow, and N. We predicted that species would perform best when environmental change matched their geographic distributional characteristics: increased temperature, snow, and N (two subalpine species), increased temperature (two dry meadow specialists), and increased snow (two snowbed specialists). Our results provided limited support for the environmental matching hypothesis. Snowbed specialists did not benefit from increased snow, dry meadow specialists' performance did not consistently differ among the treatments, and subalpine plants' survival was not affected by treatments while their growth response was variable among species. Our results suggest that global change effects will vary among species and distributional shifts are not easily predicted by species environmental preference.

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Distributional shift; climate change; global change; alpine plants; subalpine plants

Introduction

The sixth assessment report of the Intergovernmental Panel on Climate Change (IPCC) outlined the many rapid and ongoing changes in the Earth's climate system, including increases in temperature and altered precipitation patterns. Earth's mean land surface temperature has increased 1.59°C from 1850–1900 to 2011–2020 (IPCC 2021). Global precipitation has increased overall but with key regional differences, including decreases in some regions such as western North America, North Africa, and the Middle East (IPCC 2021). In addition to climate change, humans have altered key global biogeochemical cycles and the distribution of key nutrients such as nitrogen (N) and phosphorus. Despite some effort and success in reducing acid rain, wet and dry N deposition driven by human transportation and agricultural sectors remains elevated or has even recently increased in many parts of the world (Ackerman, Millet, and Chen 2019). Though there have been many studies on individual global change factors, there is a need for more studies on how simultaneous changes in multiple factors affect biota across the tree of life and how these scale up to whole ecosystem responses (Komatsu et al. 2019; Rillig et al. 2019; Zhou, Gu, and Smaill 2023). Despite much previous work on individual species responses to environmental change, there is also a need to test generalizable frameworks and hypotheses for how species respond to environmental change.

Mountainous regions are particularly affected by warming, changes in snowpack, and nitrogen pollution, in terms of both the magnitude of the change and the sensitivity of ecosystems to the change. For example, temperatures are warming at faster rates in many mountainous regions compared to lowlands (Pepin et al. 2015, 2022), and cold-adapted plant and animal species are more vulnerable to such change than more generalist species (Grabherr, Gottfried, and Pauli 2010; Stewart, Wright, and Heckman 2017). Important winter

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snowpack, which provides insulation in the winter and water during the summer and governs alpine plant community composition (Suding et al. 2015; Rixen et al. 2022), is also changing, with evidence of increases in some regions (Leffler and Welker 2013) and decreases in others (Mote et al. 2018). Alpine ecosystems are considered one of the most sensitive ecosystems to N deposition due to their limited ability to take up and neutralize excess N (Bowman et al. 2015).

Distributional shifts can help organisms cope with changing environmental conditions by "tracking" suitable conditions. Distributional shifts could involve either shifting a latitudinal or elevational limit at the edge of the geographic range (i.e., range shift or "beyond-range distributional shift") or occupying new areas within the geographic range but in different microclimates (i.e., "within-range distributional shift" or "landscape position shift"; Figure 1). A within-range distributional shift for plants is similar to the idea of utilization of distribution shifts within a home range of an animal (Clapp and Beck 2015). Uphill range shifts under warming conditions are one way in which species can take advantage of the environmental lapse rate to disperse to more favorable conditions under climate warming (I.-C. Chen et al. 2011). Shifts are anticipated and have already been observed across multiple ecotones: subalpine species (shrubs and herbaceous species) have moved uphill into the alpine (Lenoir et al. 2008), tree line has moved upwards (Harsch et al. 2009), and alpine tundra has moved uphill into previously unvegetated soils (Bueno de Mesquita, Tillman et al. 2018). Lastly, alpine and subalpine species are expected to experience range contractions at their lower elevation limit (Pauli et al. 2007; Pérez-García et al. 2013; Freeman et al. 2018), which will lead to a loss of habitat because even if they shift their range uphill, surface area decreases at higher elevations (Elsen and Tingley 2015), although this is partially buffered by the high diversity of microhabitats on mountains (Rixen and Wipf 2017).

For vegetation in mountainous regions, uphill range shifts are often not solely dictated by latitude or elevation but are also affected by topographic heterogeneity. In mountainous regions that are characterized by steep elevational gradients as well as a high degree of heterogeneity in topography, microclimates, snowpack, and soil moisture (Suding et al. 2015; Hermes et al. 2020), species occupation of new areas within the geographic range but in different microclimates could be an important process (Bueno de Mesquita, Tillman, et al. 2018; Körner and Hiltbrunner 2021). Slope and aspect exert major influences on local air and soil temperatures, such that microclimates located only several meters apart may be more different in temperature than some locations tens of meters uphill or hundreds of meters away in latitude (Graae et al. 2018; Körner and Hiltbrunner 2021). In this way, topographic heterogeneity and associated microclimate could provide "microrefugia" for plants under global change (Maclean et al. 2015; Suggitt et al. 2018).

In all cases, whether within or beyond the current range, whether or not a species can establish in a new geographic location or landscape position depends on multiple processes such as dispersal, germination, and establishment. These processes are affected by local environmental conditions such as temperature and moisture (Kueppers et al. 2017), as well as biotic

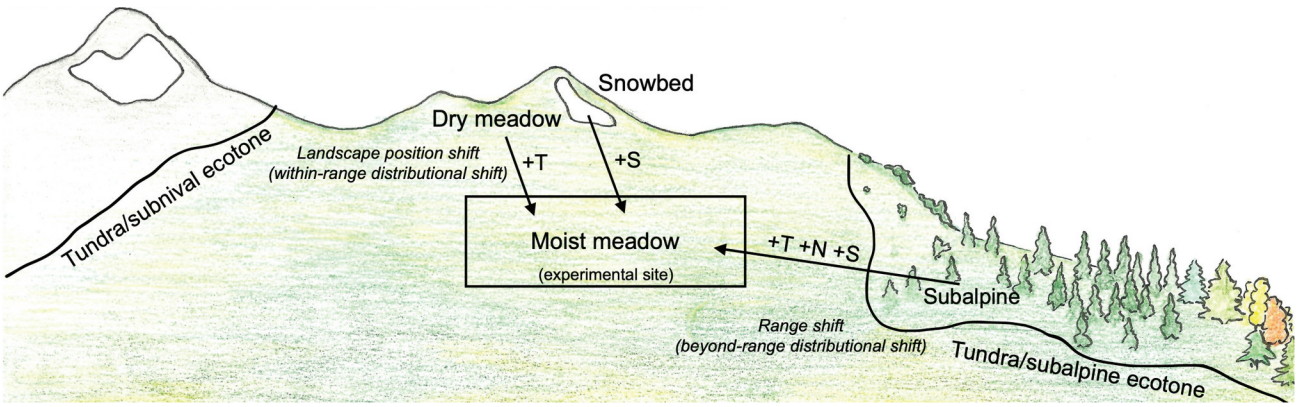

Figure 1. Conceptual diagram of local species distributions and predictions for how global change may affect shifts within (landscape position shift, also referred to as within-range distributional shift) and across (range shift, also referred to as beyond-range distributional shift) ecotones. Subalpine species moved to moist meadow are predicted to perform best with increased snowpack (+S), nitrogen (+N), and temperature (+T); dry meadow species moved to moist meadow are predicted to perform best with increased temperature (+T); and snowbed species moved to moist meadow are predicted to perform best with increased snowpack (+S). Background illustration by Jane G. Smith. Habitats at Niwot Ridge also include wind-blown "fellfields" on knoll summits, as well as "wet meadows" immediately below snowbeds.

interactions (competition, facilitation) within and across trophic levels (Hillerislambers et al. 2013; van der Putten et al. 2016; Bueno de Mesquita et al. 2020; Shay et al. 2021). An example of facilitation is that subalpine species are often found in the low alpine near shrubs, which create microclimates with warmer temperatures in winter due to increased snowpack (Brigham 2022). It is unknown whether the observed positive association between subalpine species and shrubs is due to facilitation via increased snowpack or facilitation via other mechanisms (soil, light, temperature, moisture) or whether both types of plants preferentially establish in the same microclimates above treeline (Brigham 2022; Brigham and Suding 2023).

Regional and local environmental variation makes it challenging to predict how species will change their local distribution in response to global environmental change. One hypothesis, which we term the "environmental matching hypothesis," posits that the environmental characteristics of a resident population and the environmental characteristics of a potential community in which that population could establish should match. This hypothesis underlies most species distribution models, because such models are built upon species–environment relationships, geospatial data, and climate forecasting (Elith and Leathwick 2009), and it is foundational to conservation planning, restoration ecology, and assisted migration and is similar to the climate matching hypothesis for invasive species (Cardador et al. 2022). For instance, if global change causes a particular site to get drier, then species from a drier community might be able to establish in the new site that is now drier even if they were not previously present there. This hypothesis also underlies observed and predicted uphill range shifts for plants, because it predicts that plants will "track" their temperature preferences (Corlett and Westcott 2013). This assumption is also the basis of a large investment in bioclimatic envelope model-based assisted migration programs and, as such, is of considerable practical importance (Stanturf, Ivetić, and Kasten Dumroese 2024). However, if changes in multiple environmental factors result in trade-offs in colonization success or other non-climate factors (e.g., biotic, soils development), this might limit colonization irrespective of environmental match (Preston et al. 2008).

Here we tested the environmental matching hypothesis using a manipulative temperature/snowpack/nitrogen addition experiment combined with transplantation of four alpine plant species and two subalpine plant species. Increased temperature and nitrogen treatments were designed to mimic the effects of climate change and nitrogen deposition, and the increased snowpack treatment was designed to mimic the effects of shrubs in the alpine. The four alpine species included two species commonly found in drier hillslope shoulders that accumulate less snow and two species commonly found in wetter toeslope areas that accumulate deep snowbeds. Utilizing these six species and three source habitat types, we tested the environmental matching hypothesis.

Based on the environmental matching hypothesis, we predicted that increases in temperature, snowpack, and nitrogen would facilitate survival and growth of the subalpine species (Figure 1). Cold temperature is a key factor limiting subalpine plants at the upper end of their elevational range (Yu et al. 2017), and thus alleviating this limitation with an increase in 1°C is expected to increase survival and growth. Although lower snowpack may be more intuitively predicted to increase subalpine plant performance in the alpine, we hypothesized that increased snowpack would actually be beneficial. Subalpine plant species are often found near shrubs (Anthelme, Villaret, and Brun 2007; Xu et al. 2010), which can increase snowpacks on their leeward and windward sides (Essery and Pomeroy 2004; Pomeroy et al. 2006) at their upper elevational limits. Shrubs also affect other factors such as soil decomposition and nutrient cycling, light availability, and moisture deficits that are not mimicked by snow fences. Shrubs can limit photosynthesis of subalpine plants in the absence of moisture limitation but can help ameliorate moisture stress later in the growing season (Dona and Galen 2006). At our field site, experiments with shrubs have shown that they can potentially facilitate subalpine plant colonization by reducing freezing degree days and increasing soil moisture (Brigham 2022). Lastly, despite the presence of recalcitrant lignin in wood, nutrient cycling rates are generally higher in the subalpine compared to the alpine due to increased temperatures and microbial activity (Salinas et al. 2011), so increases in N availability may be expected to benefit subalpine plant establishment in the alpine.

As for the alpine species, we expected the dry meadow species to perform best (i.e., higher survival and growth) without nitrogen or snow addition but with increased temperature, because this could lead to drier conditions that are typically also associated with higher soil temperatures. We expected the snowbed specialist species to perform best with increased snowpack and without increased nitrogen or warming (Figure 1).

Methods

The experiment was conducted from 2016 to 2021 in moist meadow alpine tundra on the north slope of Niwot Ridge, Colorado (40°03′ N, 105°35′ W) just above tree line at 3,400 m.a.s.l. Alpine tundra is

characteristic of the region, with short growing seasons from June to August, cold snowy winters from October to May, and a high degree of topographic heterogeneity and wind-distributed snow. Climate data from the nearby Saddle meteorological station indicate average summer (1 June–31 August) temperatures of 10.3°C and an average summer precipitation of 151 mm for the years 2016 to 2021 (Morse, Losleben, and Niwot Ridge 2023; Morse and Niwot Ridge 2023). Niwot Ridge has experienced increased air temperatures over the past several decades (McGuire et al. 2012; Bueno de Mesquita, Tillman et al. 2018). Furthermore, precipitation has been changing, with slightly more winter precipitation in the alpine but still lower snow water equivalent in the subalpine, earlier snowmelt in the alpine, and earlier ice-off dates in alpine lakes (Jepsen et al. 2012; Kittel et al. 2015; Christianson et al. 2021). Nitrogen deposition peaked in 2000 and declined to ~10 kg ha^{-1} yr^{-1} (Litaor et al. 2018) but is still above estimated critical loads for alpine plant communities here of 4 kg ha^{-1} yr^{-1} (Bowman et al. 2006).

In 2006, a multifactor manipulative global change experiment was initiated in moist meadow tundra on the north slope of Niwot Ridge, with 48 1 × 1 m plots established across three blocks (Figure 2, Figure S1; Smith et al. 2012; Farrer et al. 2014; Collins et al. 2022). Each block was split by a 10-m-long by 1-m-tall snow fence erected along a north–south line from September to June, such that eight plots on the leeward side "subblock" received increased snow (+S) and eight plots on the windward side "subblock" received ambient snow. Snow measurements in 2007–2008 found an average of 50 cm more snow on the leeward side in the spring and increased the depth of early season snowfall events in the fall, creating a total of six to eight weeks more snow cover on the leeward side of the fence (Smith et al. 2012). This effect of the snow fence approximately mimics the effects of alpine shrubs (*Salix* spp.) on snowpack at this site, where alpine shrubs have been increasing over time (Formica et al. 2014; Bueno de Mesquita, Tillman et al. 2018). On each side of the snow fence, eight 1 × 1 m plots were established in two rows of four plots, 1 to 4 m from the snow-fence, and were randomly assigned one of four treatments: a warming treatment (+T) with an open-top "ITEX" chamber (following methods of the International Tundra Experiment;

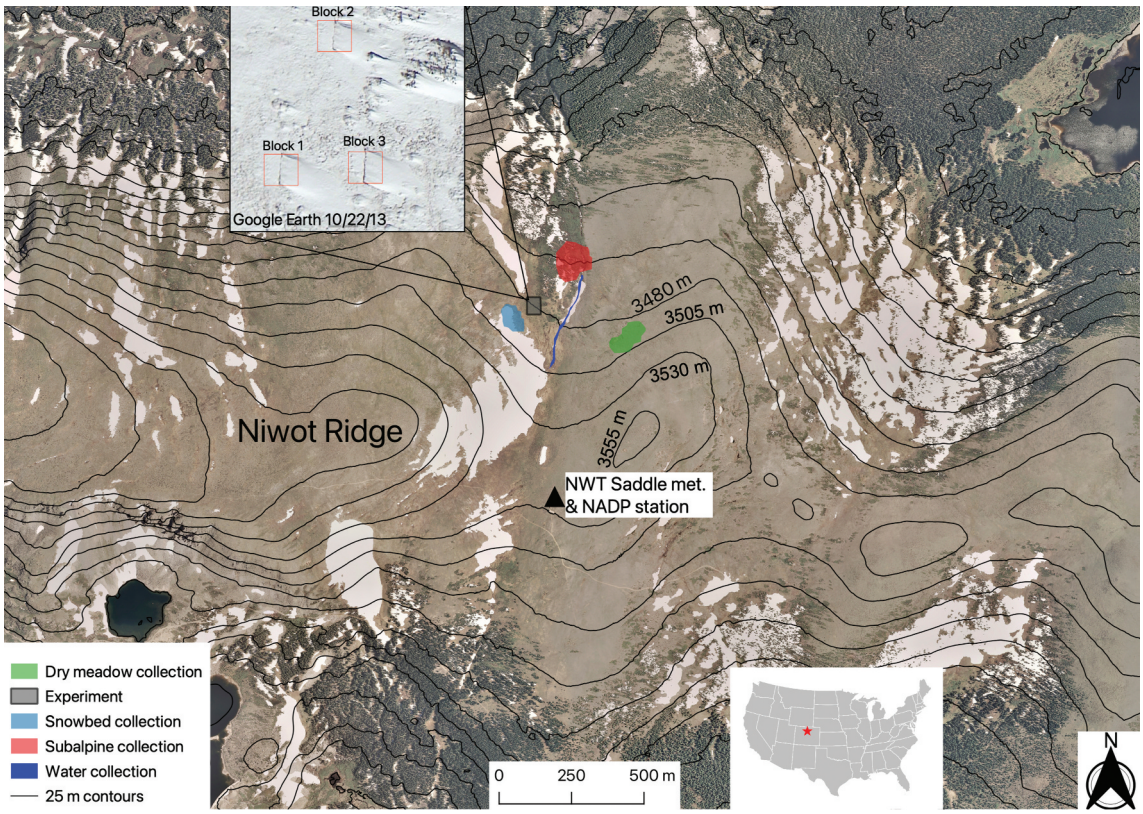

Figure 2. Map of the experimental field site and transplant collection sites on Niwot Ridge, Colorado. Also shown are 25-m contour lines and the seasonal snowmelt stream where water was collected to water transplants following transplantation in 2016. Background imagery is at 0.6-m resolution from aerial orthophotography taken in July 2008. The inset shows the arrangement of the blocks as well as the buildup of snow on the leeward side of each of the three snow fences (one per block), similar to the buildup of snow on the leeward sides of shrubs and krummholz, from a satellite image taken on 22 October 2013.

Henry and Molau 1997), an N fertilization treatment (+N) with slow-release urea nitrogen at a rate of 28 g m^2 yr^{-1} from 2006 to 2010 and 10 g m^2 yr^{-1} from 2011 to the present, a combination warming and fertilization treatment, or none (control). The ITEX chambers resulted in +1°C air temperature and +0.5°C soil temperature in 2007 (Smith et al. 2012). In addition to those effects on temperature, ITEX chambers have important side effects such as blocking wind (Hollister et al. 2023). It is also possible for ITEX chambers to create overnight cold sinks and lower minimum temperatures compared to control plots; alternatively, ITEX chambers can still increase minimum temperatures but to a lesser degree than mean and maximum temperatures (Hollister et al. 2023). ITEX chambers were erected following snowmelt in the spring and taken down at the end of the growing season. This avoided any effects of ITEX chambers on snowpack. The amount of nitrogen made available by the N treatment is less than 8 g m^2 yr^{-1} due to surface water flow. Nitrogen availability was measured with ion exchange resins at 10-cm depth in the winter 2011–2012 and summer 2012 and confirmed increased nitrogen availability in the +N treatment. For example, winter resin N averaged ~34 mg m^{-2} d^{-1} in +N plots and only ~3 mg m^{-2} d^{-1} in control plots (Farrer et al. 2015). The result of the treatment and the snow fences is a factorial design with control and additions of one variable, two variables in combination, or all three variables in combination, which will be defined as +S, +N, +T, +SN, +ST, +NT, and +SNT. These manipulations have been maintained annually from 2006 to the present (Figure 1). All 1 × 1 m plots were trenched to 15 cm twice every summer to reduce root in-growth from adjacent tundra.

In July 2016 we transplanted plugs of nearby adult individuals of six different herbaceous plant species into the forty-eight plots (Figure 2), in a row in the last 10 cm next to the edge of the plot, with one individual per species per plot (i.e., n = 48 for each species). Plugs were dug and extracted with a Hori Hori trowel and contain an individual plant with aboveground and belowground parts and soil, approximately 5 cm wide × 5 cm long × 10 cm deep. The six species are the alpine dry meadow specialists *Tetraneuris acaulis* and *Erigeron pinnatisectus*, the alpine snowbed specialists *Ranunculus adoneus* and *Micranthes rhomboidea*, and the subalpine species *Trollius albiflorus* and *Polemonium pulcherrimum*. These six species were chosen because they are all forbs (to focus our tests on the same functional group), are some of the most abundant forbs in their respective habitats, and are all found nearby the experimental site. The source locations are nearby but differ from the transplant site. The "snowbed" source site contains a large snow field that melts out several weeks later than the transplant site. Thus, the snowbed site has a shorter growing season than the transplant site. Because it is on a slope and contains less plant cover and soil organic matter, the snowbed site generally holds less soil moisture than the transplant site apart from the time period immediately following snowmelt. The "dry meadow" source site is on a windswept knoll and is considerably drier than the transplant site, the snowbed site, and the subalpine site. The "subalpine" source site is about 25-m elevation below the transplant site and contains populations of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). Other work on Niwot Ridge has suggested that subalpine soils may have similar soil moisture levels as dry meadow soils, which are less than half of those of moist meadow soils on average (Y. Chen et al. 2020). However, the specific subalpine source site included both drier upland areas (for *P. pulcherrimum*) as well as wet riparian areas (for *T. albiflorus*). Subalpine soils at Niwot Ridge are also characterized by lower pH, greater C:N ratio, lower N mineralization rates, and lower nitrification rates than dry meadow and moist meadow soils (Y. Chen et al. 2020). The subalpine species are occasionally observed in the alpine but at our field site this has only been observed to occur next to shrubs or krummholz. Transplants were watered every other day after transplanting for two weeks with water from a nearby natural stream of snowmelt water to minimize transplant shock. Survival, leaf number, longest leaf length, and height were measured annually at peak biomass in 2017, 2018, 2019, and 2021. 2020 was skipped due to the COVID-19 pandemic. In 2021 the experiment was concluded and all surviving individuals were harvested and biomass was dried and weighed. Twenty individuals of each plant were harvested nearby in 2016 to calculate allometric relationships between biomass and the measured variables. However, allometric relationships were weak and therefore we did not test for effects of the global change factors in 2016 to 2019 or compare allometric biomass to the true biomass measurements done by aboveground harvest in 2021. For growth metrics in 2016 to 2019, we use leaf number and longest leaf length, which are two variables that are generally positively correlated with plant growth. Across the whole data set (all species combined), longest leaf length and leaf number were negatively correlated (r = −0.07, p = .02). Soil moisture in all plots was measured on 4 August 2016 and 9 September 2016 with a handheld HydroSense II probe.

Survival across all years for each species was analyzed with mixed effects survival models in the *coxme* R package (Therneau 2022), with plot nested in block as a random effect and temperature, snowpack, and nitrogen as fixed effects. Temperature, snowpack, and

nitrogen were tested as either categorical variables based on the assigned treatment (static over time) or as calculated continuous variables using nearby temperature, nitrogen, and snow measurements collected from the Saddle site on Niwot Ridge (incorporating annual differences but data available only for 2016–2019; Collins et al. 2022). The effects of the global change factors on 2021 weighed aboveground biomass and 2016 soil moisture were tested with a similar mixed effect model but with subblock nested in block as the random effect, because there was no need to take into account repeated measures at the plot level; this was implemented in the *lme4* R package and followed by Type III analysis of variance (Satterthwaite's method) in the *lmerTest* R package (Kuznetsova, Brockhoff, and Christensen 2017). Interactions among global change factors were not included in the survival models to enable testing of all species, though they were included in biomass models for the four species with the highest survival. The effects of temperature, snowpack, and nitrogen on log-transformed longest leaf length and number of leaves were tested with the three categorical variables, year, and univariate interactions with year as fixed effects and plot nested in block as a random effect. All figures showing data were made with the *ggplot2* R package (Wickham 2016). All statistical and graphical analyses were performed with R v4.2.3 (R Core Team 2023). Data for the transplant experiment as well as the rest of the larger global change experiment are publicly available via the Environmental Data Initiative (Suding, Smith, Ashton, and Niwot Ridge 2023).

Results

Survival

Overall survival ranged from 2 to 79 percent for the six species after the six years (Figure 3). The two snowbed species had the highest survival, with >75 percent of individuals surviving over the course of six years. There was a great disparity between the two subalpine species, with *T. albiflorus* surviving at a rate of 69 percent and *P. pulcherrimum* experiencing high mortality, with only one individual surviving to 2021 (2 percent). The two dry meadow species also had lower survival than the snowbed species, with *E. pinnatisectus* at ~33 percent survival and *T. acaulis* at only 4 percent survival (two individuals). These two dry meadow species experienced most of their mortality in 2017, the first summer after transplanting. Most individuals were still alive by the end of the growing season in 2016 (the same summer in which they were transplanted), so this was not a case of transplant shock causing immediate mortality.

Effects of the global change factors on plant survival over time varied depending on species and source habitat type (Table 1, Figure 4, Figure S2). Increased snowpack significantly negatively affected survival of one of two snowbed species (*R. adoneus*) and one of two dry

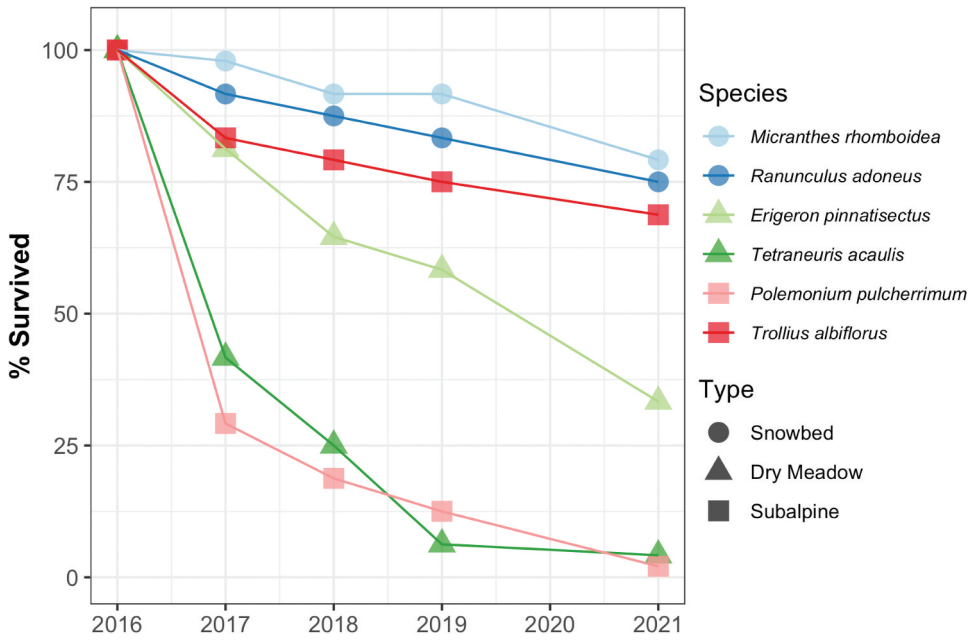

Figure 3. Descriptive summary of survival for each of the species over time, aggregating all controls and treatments for each species. For statistical results on the effects of snow, nitrogen, and temperature on the death rate of the species, see Table 1 and Figure 4. Snow addition had significant negative effects on *R. adoneus* and *T. acaulis* survival, and warming had a significant positive effect on *M. rhomboidea* survival.

Table 1. Summary of main effects using categorical variables.

Model	Type	Species	Snow	N	Temp.	Year	Int.
Survival	Snowbed	MICRHO	n.s	n.s.	*(-)		
	Snowbed	RANADO	**(-)	n.s.	n.s		
	Dry meadow	ERIPIN	n.s.	n.s.	n.s.		
	Dry meadow	TETACA	*(-)	n.s.	n.s.		
	Subalpine	POLPUL	n.s.	§(+)	n.s.		
	Subalpine	TROALB	n.s.	n.s.	n.s.		
2021 Biomass	Snowbed	MICRHO	n.s.	*(-)	n.s.		n.s.
	Snowbed	RANADO	n.s.	n.s.	n.s.		n.s.
	Dry meadow	ERIPIN	n.s.	n.s.	n.s.		n.s.
	Dry meadow	TETACA					
	Subalpine	POLPUL					
	Subalpine	TROALB	n.s.	§(+)	n.s.		n.s.
Longest leaf	Snowbed	MICRHO	n.s.	n.s.	*(+)	***(+)	n.s.
	Snowbed	RANADO	n.s.	§(+)	n.s.	***(+)	n.s.
	Dry meadow	ERIPIN	n.s.	n.s.	**(+)	**(-)	n.s
	Dry meadow	TETACA	§(-)	n.s.	n.s.	***(-)	n.s.
	Subalpine	POLPUL	**(-)	*(-)	***(+)	***(-)	Y:S**, Y:N*, Y:T***
	Subalpine	TROALB	**(+)	§(+)	§(+)	***(+)	n.s.
Leaf num	Snowbed	MICRHO	n.s.	n.s.	n.s.	n.s.	n.s.
	Snowbed	RANADO	*(-)	n.s.	n.s.	§(+)	Y:T §
	Dry meadow	ERIPIN	n.s.	§(-)	n.s.	***(-)	n.s
	Dry meadow	TETACA	n.s.	n.s.	§(-)	***(-)	Y:T §
	Subalpine	POLPUL	n.s.	**(-)	*(-)	***(-)	Y:S*, Y:N**, Y:T***
	Subalpine	TROALB	n.s.	n.s.	*(-)	n.s.	n.s.

Notes. Survival is the survival rate over time (how quickly individuals died). Interactions among global change variables were tested for biomass. Year was included as a variable for leaf variables, and interactions between individual global change variables and year were tested. Survival models were fit with *coxph* and growth models were fit with *lme4*. Background colors represent whether the results were consistent with predictions; blue = results in line with predicted positive effect, gray = results opposite of prediction, no highlight = result with no a priori prediction. (+) = positive effect (slower death rate), (–) = negative effect (faster death rate). Y = year, S = snow, T = temperature, N = nitrogen.
§$p < .10$, *$p < .05$, **$p < .01$, ***$p < .001$, n.s. = not significant, blank cells = not tested.

meadow species (*T. acaulis*) and did not affect either subalpine species. Increased nitrogen did not significantly affect either snowbed species or dry meadow species and marginally increased the survival of one of two subalpine species (*P. pulcherrimum*). Increased temperature significantly negatively affected one of two snowbed species (*M. rhomboidea*) and did not affect either dry meadow species or subalpine species (Table 1, Figure 4). Results were similar when using continuous snowpack, temperature, and nitrogen variables for 2016 to 2019 (Figure S3).

Growth

None of the three global change factors had significant effects on aboveground 2021 (year 6) biomass for the four species with sufficient sample size (>50 percent survival) for analysis, with the exception of a significant effect of +N on *M. rhomboidea* (Figure 5). Longest leaf length increased and then plateaued for both snowbed and one subalpine (*T. albiflorus*) species, whereas overall it declined for both dry meadow species (despite an initial increase for *E. pinnatisectus*) and the other subalpine (*P. pulcherrimum*) species (Figure 6a). Note that *P. pulcherrimum* experienced a major drop in longest leaf length during the first year that remained until 2019; in 2021, there was only one surviving individual, and though this individual had the longest leaf length, it should not be interpreted as an average increase in leaf length over the course of the experiment. Leaf number increased over time in the snowbed species, declined in the dry meadow species, and declined or was stable in the subalpine species, when aggregating all treatments (Figure 6b).

Similar to effects on survival, global change factors affected growth but in directions not predicted by the environmental matching hypothesis. Longest leaf length was significantly affected by temperature in three species

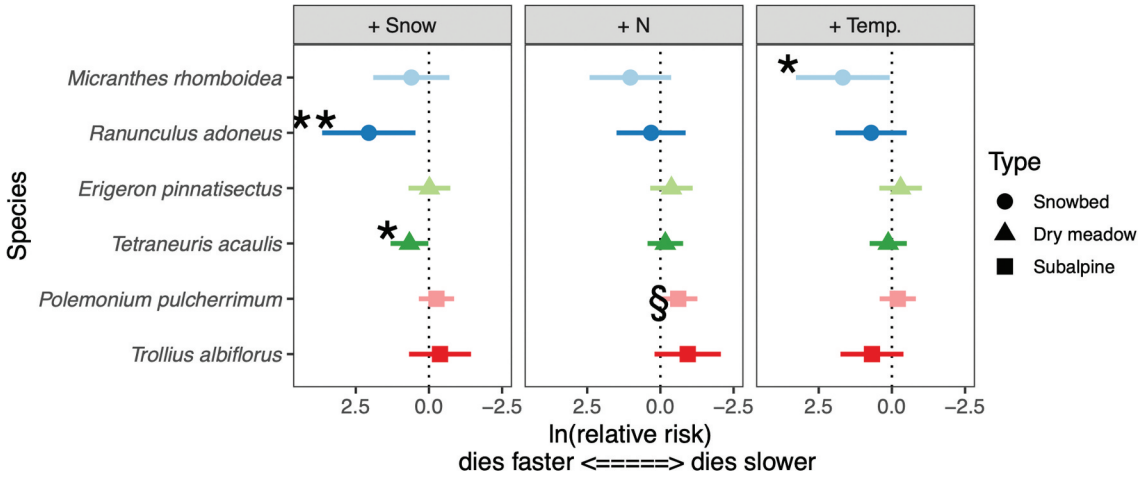

Figure 4. Main effects of increased snowpack (+S), temperature (+T), and nitrogen (+N; as categorical variables) on survival relative to controls. Results are similar to results using continuous variables (Figure S3). For statistical results, see Table 1 (*$p < .05$). Note that here the coefficients on the *x*-axis are presented right to left such that effects to the right of zero (dashed line) are *positive* (dies slower) and effects to the left of zero are *negative* (dies faster).

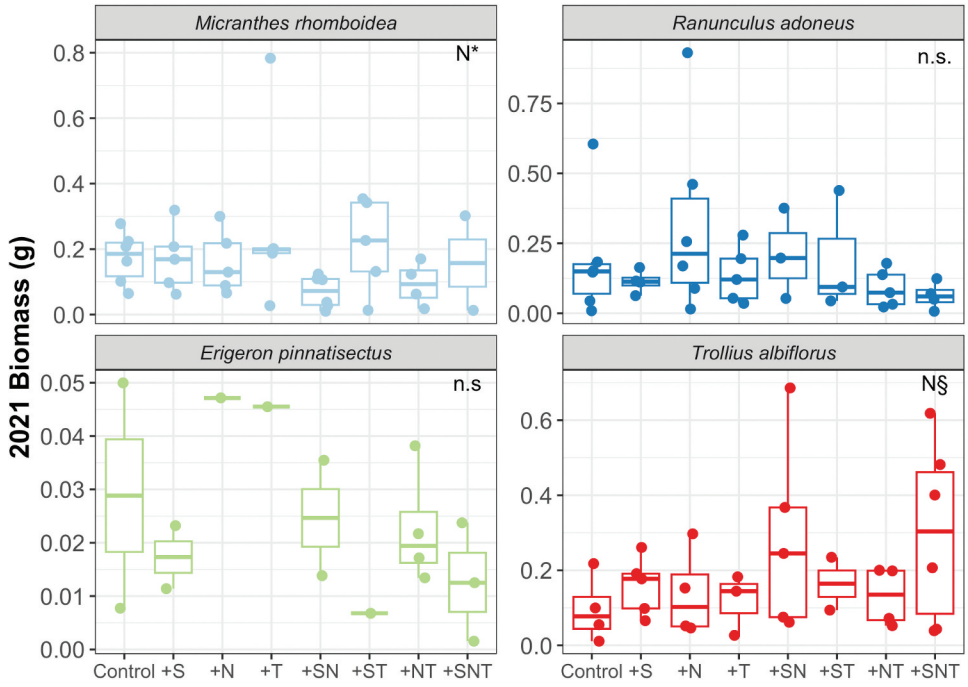

Figure 5. 2021 (sixth growing season of the experiment) aboveground biomass among all treatments for the four species with enough surviving individuals for statistical analysis (Table 1). Biomass generally was not affected by global change factors, except for a negative effect of nitrogen on *M. rhomboidea* (*$p < .05$, n.s. = not significant).

(one from each source habitat, positive effects), snowpack in two species (both subalpine species, mixed effects), and N in one species (subalpine, negative effect; Table 1, Figure 7, Figure S4). Leaf number was generally significantly affected by different variables than longest leaf length, with two species significantly affected by temperature (subalpine, negative effect), one by snowpack (snowbed species, negative effect), and one by N (subalpine, negative effect; Table 1, Figure 7, Figure S5). All significant effects of global change factors on the number of leaves were negative. In one instance, the effect of global change was the opposite on longest leaf as on leaf number (temperature for the subalpine species *P. pulcherrimum*), and in one instance it was the same (N for *P. pulcherrimum*). For the individuals that survived, global change treatments tended to increase longest leaf number relative to unmanipulated controls, whereas effects on leaf number were mixed (Figures S4 and S5).

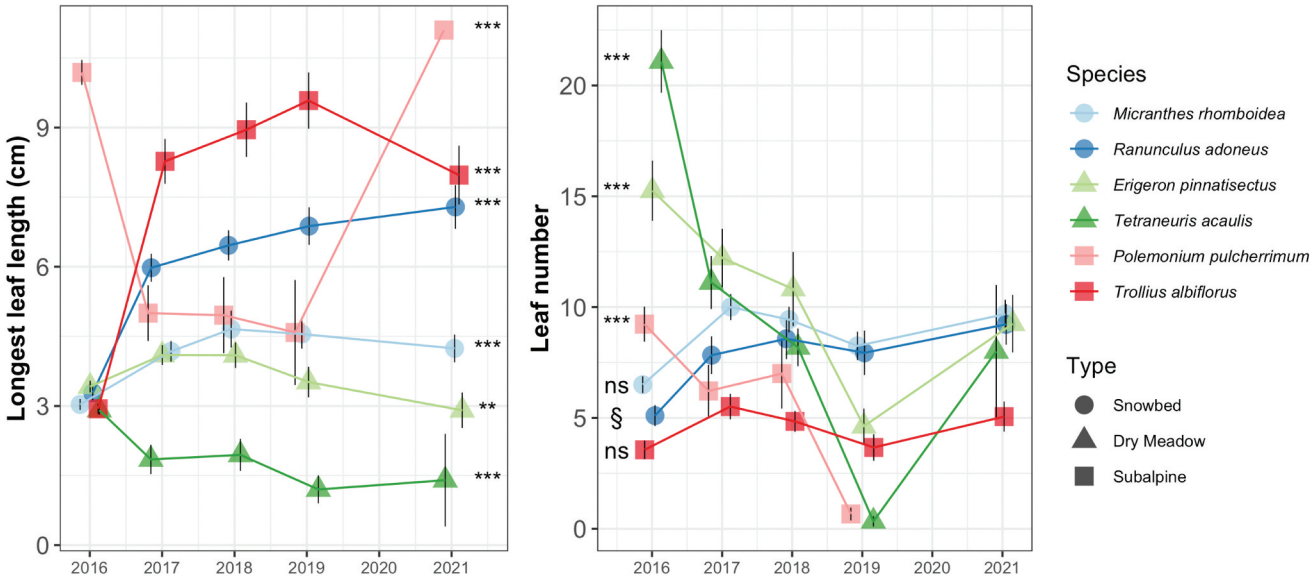

Figure 6. (a) Longest leaf length and (b) number of basal leaves aggregated across all treatments over time (year effect: §$p < .1$, *$p < .05$, **$p < .01$, ***$p < .001$, ns = not significant). Note that there was only one *P. pulcherrimum* individual and only two *T. acaulis* individuals surviving to 2021. Leaf number on the lone 2021 *P. pulcherrimum* survivor was sixty-three and is not shown. Note the difference in *y*-axis scale.

Discussion

We manipulated temperature, snowpack, and N deposition experimentally and transplanted six different species into a new position on the landscape to test how global change affected elevational range shifts (i.e., beyond-range distributional shift, two species) and landscape position shifts within the same elevational range (i.e., within-range distributional shift, four species). We tested what we refer to as the environmental matching hypothesis based on the current distribution of the species and their observed habitat preferences. Generally, the effects of the global change factors depended greatly on the species and were not always in line with predictions. Furthermore, the effect sizes were small and were mostly limited to effects on survival rather than biomass five years following transplantation. Effects on growth metrics measured annually—longest leaf length and leaf number—were not consistent except in one instance, suggesting trade-offs in those two metrics.

Beyond-range distributional shifts

We transplanted two subalpine species into the alpine to test how warming, snowpack, and nitrogen influence an upwards elevational range shift that is predicted to occur with climate change. Only one of the two subalpine species was able to survive in the alpine after being transplanted there. Though this is a much too limited sample size to make generalizations about subalpine communities as a whole, these results are an initial indication that certain subalpine species may perform better than others and perhaps colonize alpine tundra if they can successfully disperse and germinate. It is possible that the site is too wet for some subalpine species such as *P. pulcherrimum*, whose extremely low survival could also be caused by a number of other abiotic (climate, microclimate, edaphic factors) or biotic (competition, herbivory) factors. *T. albiflorus* is often observed in very wet riparian areas and performed well overall, with 69 percent overall survival. The survival rates of the subalpine species were not clearly lower than those of the alpine species because there was a lot of variation among the six species regardless of origin and more species would need to be tested to make generalizations about alpine versus subalpine species. The seeds of the two species are relatively large compared to alpine plants and not easily carried long distances by wind, so it remains unclear how many seeds might be dispersing into the alpine. A lack of tree seeds has been found in the alpine close to tree line at our field site (Robert Andrus, Washington State University, June 1, 2023, unpublished data), and this may also be the case for herbaceous subalpine species.

None of the predictions based on the environmental matching hypothesis were supported by the data. Although some individuals did survive in the alpine, there were no significant effects of the global change factors on subalpine plant survival. There were positive effects of the global change factors on *T. albiflorus*

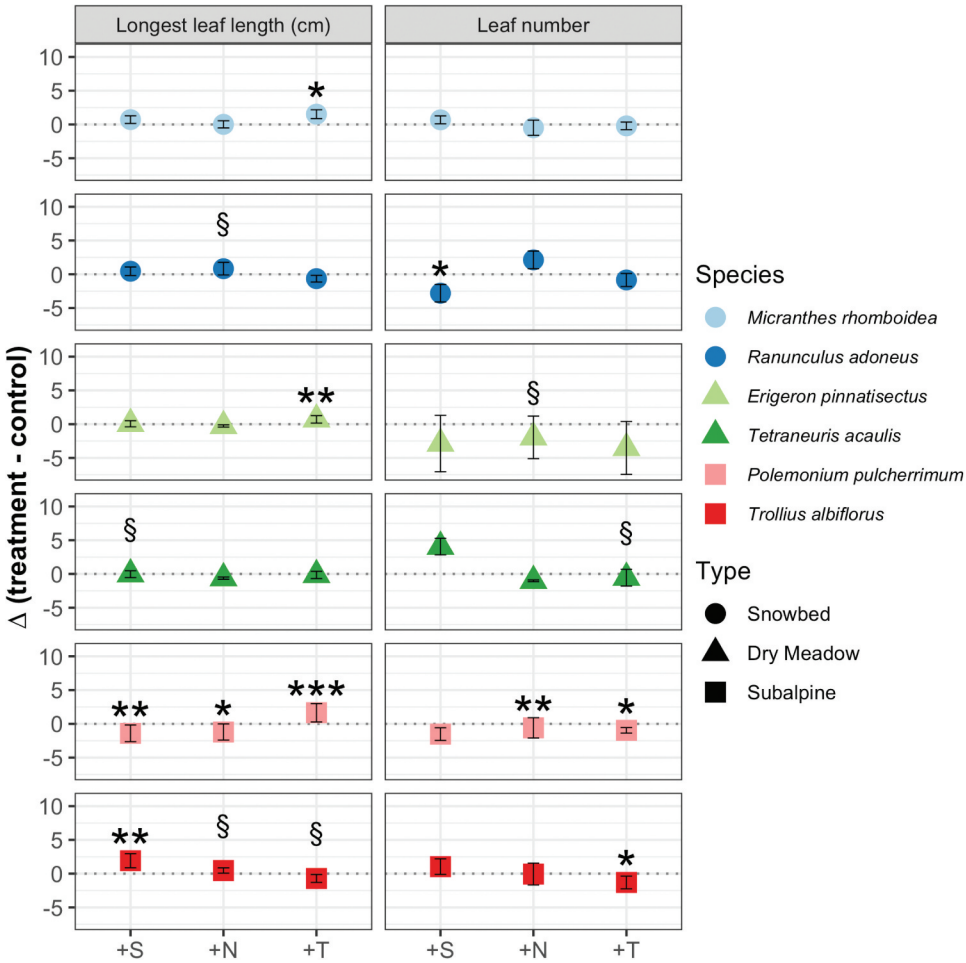

Figure 7. Change in (left) mean (±standard error) longest leaf length and (right) mean number of basal leaves between controls and treatments (treatment − control) for the three blocks, aggregated across years. Treatment main effect: §$p < .1$, *$p < .05$, **$p < .01$, ***$p < .001$). Note that there was only one *P. pulcherrimum* individual and only two *T. acaulis* individuals surviving to 2021.

longest leaf length, but these did not translate into effects for overall biomass. The high mortality observed over the course of six years may limit successful population establishment over time, because it could reach 100 percent in a few more years. Though uphill range shifts have been observed for tree and shrub species in mountainous regions (Harsch et al. 2009; Kopp and Cleland 2014; Bueno de Mesquita, Tillman et al. 2018), herbaceous subalpine plants are less well studied but communities are likely more stable in composition over time than those in the alpine (Vittoz et al. 2009). Though subalpine plants have been found to germinate in colder conditions than alpine plants and in snow-like conditions (cold, moist, dark stratification; Fernández-Pascual, Jiménez-Alfaro, and Bueno 2017), we did not observe any seedlings of these species growing nearby the transplants, suggesting little to no natural recruitment during the course of the experiment; some individuals were observed to make flowers, but we did not measure seed set. Despite broad relationships between elevation and decomposition rates, alpine meadows and the upper subalpine dwarf forests have similar decomposition rates, such that N addition may not have much effect on subalpine plant establishment in the alpine (Wang, Ruan, and Han 2010). Furthermore, at our site the considerably higher soil C:N ratio in the subalpine than in the alpine is associated with lower mineralization and nitrification rates (Y. Chen et al. 2020), such that subalpine plants are likely adapted to lower N availability than in the alpine. Similarly, these subalpine plants might be adapted to lower (*P. pulcherrimum*) or higher (*T. albiflorus*) soil moisture levels that characterize the specific subalpine areas in which they are found.

Within-range distributional shifts

We transplanted two dry meadow specialists and two snowbed specialists into a moist meadow habitat to test how warming, snowpack, and nitrogen influence

potential landscape shifts that may occur in landscapes with topographic heterogeneity under different global change scenarios. According to the environmental matching hypothesis, dry meadow species are expected to survive and grow in a moist meadow habitat if temperatures increase and snowpack decreases (both of which create drier conditions), whereas snowbed species are expected to survive and grow if snowpack increases. Landscape shifts could be important for species persistence; in areas in which climate change is decreasing snowpack, snowbed communities are at the most risk of negative impacts (Matteodo et al. 2016).

There was no support for the environmental matching hypothesis for survival and weak partial support for growth. There were some significant effects of global change factors on snowbed plant survival, but these were not consistent across the species of the same type. For instance, *R. adoneus* experienced faster mortality in plots with increased snowpack despite its status as a snowbed specialist. Furthermore, *M. rhomboidea* experienced faster mortality with warming, which was not expected a priori. It is possible that the site is still simply too moist for dry meadow species even in the increased temperature treatment.

The biomass of dry meadow and snowbed species measured in 2021 after five growing seasons in the moist meadow was not significantly affected by global change factors. There were, however, several significant effects on leaf length and number, which were measured every summer. However, these effects were highly variable and often were not in the direction predicted by the environmental matching hypothesis (Table 1). For instance, the snowbed specialist *R. adoneus* grew longer leaves over time but grew fewer leaves with increased snowpack, contradicting the hypothesis. The dry meadow specialist *T. acaulis* grew fewer leaves over time and with increased temperature, also contradicting the hypothesis. The variable responses of leaf number and leaf length, as well as the potentially compensatory dynamics between these measurements, partially explain the general lack of effect of global change factors on aboveground biomass.

Soil moisture is an important characteristic that varies across habitat types and thus across the three source sites and the transplant site. Although we had the initial expectation that drier conditions would occur in warmer conditions (and this would favor dry meadow species establishment), treatment effects on soil moisture are likely to be much more complex and dynamic than that. For example, soil moisture was lower in increased temperature plots on 9 September 2016 but not on 4 August 2016, perhaps due to a rain event or enough snowmelt water arriving from upslope (Figure S6). Furthermore, ITEX chambers can have variable effects on soil moisture—increases in temperature can decrease soil moisture but decreases in wind can increase soil moisture (Hollister et al. 2023). There was also a large effect of block on soil moisture on those dates (Figure S6); this may have made it more difficult to detect responses to the global change factors in this experiment.

Overall, the results of our simulated position shift in alpine plants via a combination of transplantation and global change treatments highlight the high degree of species specificity in responses, both among and within habitat preferences, and the difficulty in predicting responses to global change. Previous work from long-term experiments and vegetation monitoring at our field site found nondirectional changes in plant communities over time, despite directional changes in regional climate patterns (Spasojevic et al. 2013). The same study found no evidence for shifts in community types (e.g., moist meadow to dry meadow), which is consistent with our results. Together our results suggest that major shifts in community composition may be slow to occur and perhaps require much longer timescales.

Other factors

Our results provide little support of the environmental matching hypothesis across the six species studied and suggest that other factors may be key considerations when predicting how species distributions may shift with global change. Specifically, interactions with microbial communities, herbivores, and other plant species, as well as variation among individuals within the same species, could influence both range shifts and landscape position shifts (Hillerislambers et al. 2013).

Tree seedlings have been shown to perform better in tundra meadow soil compared to unvegetated soil, suggesting a role of edaphic properties, including soil biota, in range shifts (Hillerislambers et al. 2013). We transplanted complete plugs containing the plant as well as the root system, root-associated microbes, rhizosphere soil and microbes, and some bulk soil and microbes. However, these microbial communities have been shown to change within the first two years following transplantation, with initial site differences becoming more homogenized (Bueno de Mesquita et al. 2020). Subalpine, dry meadow, snowbed, and moist meadow communities have distinct soil microbial communities (Bueno de Mesquita, Sartwell et al. 2018; Porazinska et al. 2018) but the potential effects of any plant–soil feedbacks that occurred following transplantation of plugs into moist meadow soils with moist meadow microbial communities were not examined here. Such plant–soil feedbacks have been studied in a similar

context of alpine plant shifts uphill to unvegetated soils, in which negative to neutral feedbacks were observed (Bueno de Mesquita, Schmidt, and Suding 2019), with more negative feedbacks in sites with low plant density and richness (Luecke et al. 2022).

We observed some evidence of herbivory on some of the species, similar to what was found in a simulated high-alpine range shift at this site (Bueno de Mesquita et al. 2020). Alpine herbivores are numerous and include pikas, marmots, elk, moose, snowshoe hares, and mountain goats. In this case, herbivores likely included the pika, because they inhabit nearby talus areas, and elk, who ate *T. albiflorus* in particular.

Competition with established alpine plants in dense meadows is another factor that could inhibit establishment of subalpine plants. However, the opposite has been shown for a treeline tree species at our site (*Picea engelmannii*), which had *lower* seedling survival when alpine plant neighbors were removed (Jabis, Germino, and Kueppers 2020). More work needs to be done on herbaceous subalpine colonization of the alpine and to see how it compares to tree and shrub colonization of the alpine. In the established moist meadow community, certain species increased and decreased in abundance and biomass with increased snowpack or temperature (Farrer et al. 2014, 2015). The total aboveground net primary production (ANPP) also varied across treatments, with high ANPP in plots that received increased snow in the absence of warming (Farrer et al. 2015). Total ANPP, in addition to potential interspecific interactions, could be indicative of increased competition and is another factor that could influence the success of the transplanted individuals (Michalet, Delerue, and Liancourt 2023).

Lastly, another factor to consider is individual or population differences within the same species. Individuals and populations of plants of the same species that live in different regions or even different microclimates in the same region or site can exhibit significant differences in both genotype and phenotype (Eckert, Samis, and Lougheed 2008; Meade et al. 2020). For example, phenotypic traits have been measured for many species in different locations at our field site, and significant intraspecific trait variation in $\delta^{13}C$ or $\delta^{15}N$ was found for seventeen of twenty species that were sampled across multiple habitat types (Spasojevic and Weber 2021). In terms of genotype, plant populations at the upper or lower elevational range limits have been shown to either be genetically distinct or vary in the amount of genetic diversity in the population (Assis et al. 2013). In our experiment, adult plants from the same population nearby the experimental site were transplanted into the experimental manipulations, so we do not expect a high degree of variation in genotype or phenotype in transplanted individuals. Furthermore, the individuals of the subalpine species were taken from the upper end of their elevational range, which would be the individuals most likely to be successful at an upwards range expansion (Sexton et al. 2009).

Conclusions

For both landscape position ($n = 4$) and elevation ($n = 2$) shifts, our data did not strongly support the environmental matching hypothesis and instead suggested several unexpected responses to temperature, snowpack, and nitrogen additions. When examining the six species together, as well as comparing the two species pairs per starting habitat type, our data also suggest differences in both the ability of individual species to establish in a new habitat type as well as in global change factors to promote or hinder such establishment. However, our sample size is limited and thus we invite future work to test the environmental matching hypothesis. Species-specific expectations should be developed and tested. The assumption that species within broader categories (e.g., subalpine, dry meadow, snowbed) will behave similarly should also be tested.

Alpine ecosystems are undergoing substantial abiotic changes, with resulting changes in alpine plant abundance, diversity, composition, and traits. However, much of this knowledge is from plot-level monitoring over time (Elmendorf et al. 2012). Our results from these six forbs show that it is still challenging to predict how species will respond to global change, particularly when the environment is changing across several different dimensions simultaneously. This could be a critical issue for the success of assisted migration projects, especially for rare or endemic species. More work using experimental approaches, including environmental manipulations and transplant relocation used here, is needed to understand potential reshuffling of assemblages across topographically heterogeneous landscapes and ecotones.

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