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# Long-Term Alpine Plant Responses to Global Change Drivers Depend on Functional Traits

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## ABSTRACT

Forecasting plant responses under global change is a critical but challenging endeavour. Despite seemingly idiosyncratic responses of species to global change, greater generalisation of 'winners' and 'losers' may emerge from considering how species functional traits influence responses and how these responses scale to the community level. Here, we synthesised six long-term global change experiments combined with locally measured functional traits. We quantified the change in abundance and probability of establishment through time for 70 alpine plant species and then assessed if leaf and stature traits were predictive of species and community responses across nitrogen addition, snow addition and warming treatments. Overall, we found that plants with more resource-acquisitive trait strategies increased in abundance but each global change factor was related to different functional strategies. Nitrogen addition favoured species with lower leaf nitrogen, snow addition favoured species with cheaply constructed leaves and warming showed few consistent trends. Community-weighted mean changes in trait values in response to nitrogen addition, snow addition and warming were often different from species-specific trait effects on abundance and establishment, reflecting in part the responses and traits of dominant species. Together, these results highlight that the effects of traits can differ by scale and response of interest.

## 1 | Introduction

The current pace of global change is rapid and its impacts on natural ecosystems, global biodiversity and ecosystem functioning are widespread (Chapin et al. 2000; Grimm et al. 2013). Determining how global change factors will influence species diversity and ecosystem function is critical to managing ecosystems in conservation and restoration (Suding et al. 2013). Changes in species diversity and ecosystem function depend on how individual species are responding to global change factors, such as warming temperatures and drought, but predicting changes in diversity and function has been challenging due to the large number and variety of species affected by global change. For example, species responses to global changes

are often studied by documenting and predicting range shifts across broad geographic scales (Madsen-Hepp et al. 2023; Stahl, Reu, and Wirth 2014); however, local changes in abundance along with establishment and extirpation are equally important. Existing research on the dynamics of local communities to global change drivers often includes only a few species and do not scale the impact of these changes to community-level shifts (Franklin et al. 2016; Suding et al. 2008; Woodward 1992), but there are an increasing number of studies that look at species and community scale changes in response to nutrient additions (Lepš et al. 2011; Pichon, Cappelli, and Allan 2022; Siefert and Ritchie 2016; Tatarko and Knops 2018; Zhou et al. 2018). Finally, many studies focus on a single global change factor (Green et al. 2022) even though multiple changes are occurring simultaneously (Komatsu et al. 2019; Rillig et al. 2019). Thus, research linking species-level patterns to community changes across a range of global change factors is critical for advancing our understanding of global change impacts on ecosystems.

Functional traits (i.e., species characteristics that relate to growth and survival strategies) provide a powerful means for linking species responses to community changes across multiple global change factors (Funk et al. 2017), as they mediate how plants respond to global changes and ultimately influence ecosystem functions (Pacifici et al. 2017; Soudzilovskaia et al. 2013). For example, if a global change increases resource availability, such as nitrogen deposition in nitrogen-limited systems or warming in cold systems, species or individuals with trait values related to more acquisitive strategies (plants with higher specific leaf area, leaf nitrogen and/or height, which favour faster growth but lower stress tolerance) should be more likely to succeed (Lin, Zeng, and Mao 2020). On the other hand, if a global change driver increases or adds stress to a system, such as warming temperatures that could result in heat stress or drier conditions, this will likely favour species with more conservative strategies (plants with higher water use efficiency, higher leaf dry matter content and lower specific leaf area that favour slower growth and higher stress tolerance) (Damschen et al. 2012; O'Brien et al. 2017). The traits related to these global change responses also likely depend on the plant community process of interest where dispersal and establishment may require different traits than those that promote growth and survival (changes in abundance once established). These dynamics will have implications for understanding and predicting biodiversity change, as they will influence which and how many species are likely to be 'winners' (species that increase in abundance or are likely to establish) versus 'losers' (species that decrease in abundance or are likely to go locally extinct; Bjorkman et al. 2018; Kühn et al. 2021; Zettlemoyer, McKenna, and Lau 2019). This logic suggests that each global change factor should favour a unique set of traits 'response' traits, Suding et al. (2008) based on how that global change factor modifies the environment experienced by the plants in each location (Green et al. 2022).

If one or few key traits determine the winners and losers of global change, this could simplify predictions of future plant community change. While several studies have examined whether traits predict individual species responses to global change, it is also key to consider whether these trait-based responses scale up to affect community-level trait patterns, which control ecosystem functioning ('effect' traits, Guittar et al. 2016; Huxley et al. 2023; Suding et al. 2008). For example, communities made up of species with more acquisitive strategies tend to increase the rate of nutrient cycling (Lee et al. 2017) and productivity (Hagan, Henn, and Osterman 2023; Reich 2012), as high-nutrient tissues cause rapid decomposition and fast growth. Thus, if global changes favour a certain set of functional traits, some elements of ecosystem functioning are likely to change as a result. However, since ecosystem functioning depends heavily on the traits of the most abundant species (Grime 1998; Smith et al. 2020), if dominant species change in a way that is different from the responses of other species with lower abundance in the system (Collins et al. 2022), changes in community weighted means can diverge from how traits influence species-specific responses to global change (Lepš and de Bello 2023). For example, it is possible that dominant species may maintain dominance even if they do not have the functional trait values that are favoured by a particular global change factor if other competing species are kept in check by biotic interactions such as herbivory or pathogens (Wilfahrt et al. 2023). In this case, community-weighted trait shifts would be limited despite changes in the responses of some individual species. Alternatively, if a certain trait does not influence species responses to a global change factor, a dominant species with a relatively extreme trait value for that trait might change in abundance for other reasons. These reasons could include because it has some other trait that influences its response or because changing species interactions cause it to increase or decrease in abundance. In this scenario, there would be a disconnect between species-specific trait effects on abundance and changes in plot-level community-weighted means.

Alpine systems are well-suited for investigating how plant communities are responding to global change drivers as they are experiencing a variety of rapid global changes. In this synthesis, we focus on three global change factors including warming, snow addition and nitrogen addition, three major global changes affecting alpine systems. In general, alpine systems are experiencing faster temperature increases compared to lower elevations (Pepin et al. 2015) and most mountainous areas are experiencing upward migrations by plant species to track warming temperatures (Lenoir et al. 2008). While warming temperatures may decrease energy limitation during short growing seasons, this depends on soil moisture availability, as moisture is likely to become limiting when warming temperatures increase moisture stress due to evaporation in areas without surplus moisture (Bjorkman et al. 2018). Thus, responses to temperature depend on changes in precipitation and changes in annual snow accumulation have been highly variable across alpine systems, with some evidence of increasing snow depth at high elevations, but with high variation across space (Barsugli et al. 2020; Kittel et al. 2016; Jepsen et al. 2012) due to the redistribution of snow by wind (Erickson, Williams, and Winstral 2005; Litaor, Williams, and Seastedt 2008). Another key factor affecting snow depth in the alpine is the presence of shrubs, which are increasing in abundance (Bueno de Mesquita et al. 2018; Formica et al. 2014) and can create deeper snowpacks on their leeward sides. Changes in snow depth have substantial impacts on alpine plant ecology (Bjork and Molau 2018), as snow accumulation influences growing season length and soil moisture throughout the growing season (Smith et al. 2018). In Arctic and alpine systems, there is considerable species turnover across hillslope gradients between low- and high-snow areas (Oldfather et al. 2023; Suding

et al. 2015). Wind keeps exposed areas (dry meadow habitats) relatively snow-free all winter and these low-productivity habitats are characterised by temperature stress, low water availability and low nitrogen availability (Billings and Mooney 1968). Blown snow accumulates in snowbanks and snowmelt during the summer growing season enhances water and nitrogen availability in moist meadow habitats found downhill of snowbanks (Suding et al. 2015). Increasing snow accumulation is likely to increase moisture availability while decreasing the growing season length. Finally, nitrogen deposition has occurred at a rate of approximately 1–3 $g/m^2$/year, with a decreasing trend over the last 20 years (Iggy Litaor et al. 2018). Nitrogen saturation in alpine systems can have extensive impacts on plant communities, biogeochemical cycles and aquatic system health as nitrogen is often the limiting nutrient in alpine systems (Burns 2004).

Here, we synthesise six long-term experiments that have manipulated at least one global change driver (temperature, snowpack or nitrogen) in an alpine tundra environment at Niwot Ridge Long Term Ecological Research site in Colorado, USA between 1983 and 2020. Specifically, we ask two questions: First, how are species' functional traits related to their responses (i.e., changes in abundance and establishment probability) to global change factors? We hypothesise that overall, acquisitive strategies (high specific leaf area (SLA), high height, low leaf dry matter content (LDMC; Reich 2014)) will result in increasing abundance through time in nitrogen and snow addition treatments because these treatments will reduce resource limitations (nutrients and moisture, respectively). On the other hand, more conservative strategies (low SLA, high LDMC, higher water use efficiency) will succeed under warming because warming treatments will result in increased moisture stress (Bjorkman et al. 2018). We also expect that the probability of establishment will involve different traits, as that process depends more on dispersal and early growth, which may or may not be linked to acquisitive or conservative strategies (Zhang, Qi, and Liu 2018). Second, how do changes over time in community-weighted means under N addition, snow addition and warming differ from species-specific trait-based responses to these global change factors and what drives these differences? We hypothesise that community-weighted mean trait changes will be similar to species-specific trait effects on abundance and establishment; but that dominant species are likely to respond differently than the average species-level trends, creating disconnects between species-level and community-level responses.

## 2 | Methods

### 2.1 | Experiments

In this synthesis, we leverage data from Niwot Ridge Long Term Ecological Research site in Colorado, USA (hereafter 'Niwot', 40°03′ N, 105°35′ W, 3528 m.a.s.l.) where researchers have been monitoring alpine plant communities and imposing global change experiments for over 40 years (Williams et al. 2016). Over this period, Niwot has seen substantial warming (approximately 0.08°C per year), especially during summer (Oldfather et al. 2023; Kittel et al. 2024a, 2024b), changing snow depth and nitrogen deposition. To better understand how warming, snow accumulation and nitrogen deposition influence alpine plant communities, we analysed vegetation data from six experiments that manipulated at least one of these primary global change factors and that have been surveyed for at least 7 years (Table 1).

For each experiment, see the reference to the Environmental Data Initiative repository (Table 1) for detailed information on experimental and data collection methods. Briefly, all vegetation data were collected annually during the growing season (July–August) using point-intercept methods in 1 $m^2$ plots with 50–100 survey points. We only used data from experiments that consistently recorded species intersecting first or first and last positions at each survey point to ensure that changes in abundance through time are not due to changes in survey methods. Any species present in a plot but not intersecting a point was given an abundance value of 0.5% for all experiments except the Saddle because species that were present but did not intersect a point were not consistently recorded in all years of surveys of the Saddle plots. While some experiments include manipulation of multiple global change factors,

**TABLE 1** | Details of each experiment included in this analysis.

| Experiment name | Warming | Snow addition | Nitrogen addition | Experiment length |
|---|---|---|---|---|
| CoDom (Suding et al. 2022) | | | X | 16 years 2002–2018 |
| N246 (Bowman 2021) | | | X | 20 years 1997–2017 |
| Fert2010 (Farrer, Smith, and Niwot Ridge 2020) | | | X | 8 years 2011–2019 |
| New ITEX (Suding et al. 2023) | X | X | X | 14 years 2006–2020 |
| Original ITEX (Walker and LTER 2020) | X | X | | 7 years 1993–2000 |
| Saddle (Walker, Humphries, and Niwot Ridge 2023) | | X | | 37 years 1983–2020 |

*Note:* Citations indicate the datasets publicly available at the Environmental Data Initiative and years indicate the years of data which we use in the analysis.

we did not have enough experiments to examine interactions robustly, so we only use plots subjected to changes in a single global change factor.

### 2.2 | Warming

Open-top chambers were used to increase temperatures following the methods of the International Tundra Experiment (ITEX). These chambers are hexagonal with a ~1 $m^{-2}$ opening at the top (Henry and Molau 1997; Marion et al. 1997). They are installed soon after snowmelt each year and taken down at the end of the growing season. On average, the warming chambers increase daytime air temperatures by 1°C–2°C (Farrer et al. 2015; Walker et al. 1999).

### 2.3 | Snow Addition

Snow fences were used to increase snow accumulation downwind of the fence, which approximately simulates the effects of tall shrubs in the alpine. Wind on Niwot tends to come from the West, so fences are arranged facing East–West. The plots in the Original ITEX and Saddle datasets are located behind the same snow fence that is 2.8 m tall and 60 m long while the New ITEX involves three smaller snow fences (10 m long by 1 m high). In the new ITEX experiment, the snow fences increased snow depth by an average of 40 cm (Farrer et al. 2015) while the old ITEX snow fence was larger and caused greater increases in snow depth, resulting in warmer soil temperatures during the winter, later snowmelt dates and increased soil moisture (Walker et al. 1999).

### 2.4 | Nitrogen Deposition

Nitrogen was added to experimental plots either as Urea from Osmocote slow-release pellets (40-0-0; CoDom, Fert2010 and New ITEX) or as aqueous ammonium nitrate ($NH_4NO_3$) (N246). Experimental addition rates varied by experiment and through time as around 2011 there was a shift towards applying more realistic levels of nitrogen based on natural deposition rates. Nitrogen was applied at a rate of 28.8 $g/m^2$/year. in the CoDom experiment until 2008 when the rate was reduced to 14.4 $g/m^2$/year. The rate was further reduced in 2011 to 5 $g/m^2$/year. The New ITEX experiment had 28.8 $g/m^2$/year. added until 2011, when the rate was reduced to 10 $g/m^2$/year. The Fert2010 experiment had 28.8 $g/m^2$/year. applied during the first year of the experiment, but subsequent years had 10 $g/m^2$/year. applied. The N246 experiment had three levels of nitrogen addition; 2, 4 and 6 $g/m^2$/year. throughout the experiment.

### 2.5 | Trait Data

All trait measurements included in these analyses were collected in the local system. From 2008 to 2018, a variety of researchers collected plant traits on the plants at Niwot Ridge (Spasojevic, Weber, and Lter 2022). We chose not to include trait values from trait databases to avoid including trait values from individuals growing in different contexts, but this means that we did not analyse some traits that might be interesting like seed and clonal reproductive traits. In addition, we did not have trait coverage for species growing across all habitat types or experimental treatments at Niwot Ridge. We use all trait measurements (regardless of habitat type and experiment where they come from) to calculate an average value per species based on measurements from at least five individuals per species collected across a range of habitats where each species occurs. We acknowledge that various forms of intraspecific variation can be large and influence species responses to change (Henn et al. 2018; Jónsdóttir et al. 2023). However, it was not feasible to measure relevant intraspecific variation related to the effects of these experiments because we did not have measurements from treatment plots and many of the experiments analysed here have been discontinued. Therefore, we focused on interspecific variation in traits. In our analysis across the six long-term datasets (Table 1), we used nine traits that had the highest coverage for the species that occur in the vegetation datasets. These traits include Specific Leaf Area (SLA), Leaf Area, Leaf Dry Matter Content (LDMC), Leaf Nitrogen Content (%N), Leaf Carbon Content (%C), Carbon 13 isotope ratio (C13), Nitrogen 15 isotope ratio (N15), Chlorophyll Content and plant height (including reproductive structures). These traits were selected because they all relate to the leaf economics spectrum (Wright et al. 2004) or plant competitive ability (Westoby 1998) and can be related to acquisitive versus conservative plant strategies. Additionally, many have been shown to relate to plant responses to global change (Kühn et al. 2021). Trait measurements were made following standardised protocols (Pérez-Harguindeguy et al. 2013) and see Spasojevic, Weber, and Lter (2022) for a detailed description of the trait measurement process. In addition, we used principal components analysis (PCA) to reduce the nine traits into two multi-trait axes. We performed the PCA using scaled and centred trait values and used the first two PC axes for each species as additional multivariate traits where PC1 represents a leaf nitrogen/specific leaf area axis and PC2 represents a plant size and carbon investment axis and report the results of these multivariate traits in the Figures S1–S3 as the focus of this synthesis is on individual traits but understanding how traits correlate and often result in syndromes that affect responses add additional information beyond individual traits.

### 2.6 | Analyses

We first examined whether traits predicted changes in species abundance and probability of establishment through time. Because we had few records of extirpations through time and low trait coverage of species that did get extirpated, we did not have enough data to fit models of extirpation. To examine changes in species abundances through time for species that were present from the beginning and did not get extirpated, we calculated the log of the ratio between the relative abundance of a species each year after the first year of the time series and the relative abundance of that species in the first year of the time series (each species has $t$-1 log ratios). We use log ratios because these allow us to relativise changes in abundance to the starting abundance of each species so that more abundant species do not weigh more heavily in our models

due to the fact that more abundant species can show larger changes in abundance. A negative log ratio indicates a lower abundance in any given year compared to the first year of the experiment for a species in a plot. The first year of data in each experiment is either pretreatment or the first year after treatment, which we believe should be representative of unmanipulated circumstances as our experience suggests that alpine plants are long-lived and often take longer than 1 year to show responses to experimental manipulations. In addition, even if species are beginning to respond in the first year, due to the long-term nature of our data, we are still likely to detect the direction of this change. To ensure that we had enough data for each species in our analyses, we excluded any species that appeared in fewer than 3 years in any given experiment. For our main analyses, we lumped all treatments into three categories: warming, snow addition and nitrogen addition. We recognise that this is a simplification of the nitrogen addition treatments, which vary in their intensity. Because of this, we also performed a nitrogen-specific analysis described below.

To examine how plant species responded over time to the global change treatments, we fit a simple linear model for each species present in each plot and extracted slope estimates of changes in the log response ratio of abundance through time. To answer our first question about how traits relate to changes in species abundance and establishment under global change, we used linear mixed-effects models to examine the effect of traits on species responses through time in each type of treatment. We constructed one model for each trait (11 models, 9 traits and 2 PC axes) which consisted of the log response ratio as a function of year (continuous, starting at one for the second year of each experiment), species trait value, experimental treatment, along with all interactions among those variables. In addition, we included random intercepts for the calendar year as a categorical variable to account for interannual climatic variation. We also included random intercepts and slopes for each species in each plot in each experiment to account for species-specific responses through time that are not related to their trait value using the following model structure: log response ratio ~ year × trait value × treatment + (1|calendar year) + (1 + year|experiment:species:plot). This model structure allowed us to examine how species trait values influence the magnitude of their abundance change through time under the different global change factors while accounting for species-specific differences, spatial heterogeneity and annual climate variability. We use linear models because examination of the raw data did not suggest that non-linear relationships were common.

We used a similar model structure for establishment probability; however, since the establishment is binary, we used a binomial model and excluded the year term because each species in a plot time series either included an establishment event or did not. In the establishment models, we included records for all species that were absent during the first 3 years of monitoring in each plot but present in at least two of the last 3 years of a given plot as establishment events. We used these cutoffs to avoid including establishment events that may have been due to species identification inconsistencies or transient dynamics. To fit binomial models, we also needed to determine the species pool that could possibly be established in our plots but which did not establish. To do this, we used all species present in at least one other plot across all experiments, but which were absent in the given plot during the entire time series as the 'non-establishment' category. All experiments were within a range where species could feasibly disperse between plots.

Finally, to answer our second question about how community-weighted mean (CWM) changes related to species-specific responses, we examined changes in CWM trait values for each plot to compare with trait effects on species-specific responses. To calculate CWM, we used standard methods of multiplying each species average trait value by its relative abundance and summing that for all species in each plot. For our analyses, we only include plots for which we had trait values for at least 80% of the species coverage for at least 75% of the years they were measured (89% of plots). We then fit a model for each trait to assess whether CWMs changed through time and whether this change varied by treatment. We fit a separate model for each trait including time, treatment and their interaction as fixed effects, then plot nested in the experiment as random slopes and intercepts along with random year intercepts: Community Weighted Mean ~ year × treatment + (1|calendar year) + (1 + year|experiment:plot).

To determine whether dominant species' responses are related to differences between CWM changes and species-specific trait effects, we also identified dominant species in these experiments by identifying any species that had a dominance candidate index (Avolio et al. 2019) greater than 0.55. We then summarised their responses to each treatment and where their trait values fall relative to other species in the system.

### 2.7 | Analysis of Varying Nitrogen Addition Levels

Because our experiments varied in the amount of nitrogen added both between experiments and over time, we conducted additional analyses to determine whether the influence of traits on species responses varied by nitrogen addition level. To do this, we used a similar approach as our first question above but used only nitrogen-addition plots and instead of treatment type, we included experiment (as a proxy for different nitrogen addition regimes) as a fixed effect in the model (Figure S4). We use experiment as the fixed effect because two experiments vary in the amount of nitrogen added through time and one had multiple addition levels that were all low compared to the other experiments. We only performed this analysis for abundance change.

All data management and analysis were performed using R 4.2.2 (RCoreTeam 2022). Models were fit using the lmerTest package (Kuznetsova, Brockhoff, and Christensen 2017). We assessed model assumptions by plotting fitted versus residual and normal Q-Q plots. For all model results, we assessed whether the main effects were significant using type II ANOVAs with the 'Anova' function from the 'car' package (Fox and Weisberg 2019). We also extracted marginal means and trends using the 'emmeans' package (Lenth 2023) and calculated 95% confidence intervals as two times the estimate standard error to assess whether trait trends differed between treatments. Due to the number of comparisons made in these analyses, we also report *p*-values adjusted for false detection rates using methods described by Benjamini and Yekutieli (2001) in Tables S1 and S2.

## 3 | Results

### 3.1 | Plant Responses to Global Change Treatments

Overall, plant changes in abundance through time when exposed to global change treatments did not differ substantially from changes observed in control plots (Figure 1). Specifically, nitrogen addition plots tended to have more declines (55% of species-plot combinations) in species abundances through time while snow addition and control plots tended to have more increases through time (54% of species-plot combinations for both) compared to warming plots, which had balanced increases and decreases. Overall, the most frequent species (those present in at least 20 plots across all experiments) showed a range of responses in both direction and strength to the global change treatments (Figure S5).

### 3.2 | Trait Effects on Species Abundance Change

Leaf nitrogen, leaf area and leaf chlorophyll content had significant effects on species abundance change: species with lower nitrogen, smaller leaves and lower chlorophyll tended to increase in abundance over time (Figure 2; Figures S6 and S7). These trends are also reflected in the results from PCA analysis showing species with higher PC1 values tended to increase in abundance in nitrogen addition plots while species with lower PC2 values tended to increase in abundance in control plots (Figure S2). Despite the lack of a significant interaction between trait and treatment for the aforementioned traits (a significant interaction would indicate that slopes differ between treatments), some trait effect slopes in specific treatments did differ from zero. Species with smaller leaves tended to increase in abundance in nitrogen addition and control plots, species with lower leaf nitrogen tended to increase in nitrogen addition plots and species with lower leaf chlorophyll tended to increase in control plots (Figure 2).

For the interaction between trait and treatment effects, trait-driven slopes differed between treatment types only for SLA, leaf carbon and C13 isotope ratio, where the increase in abundance of species with high SLA, low leaf carbon and lower C13 isotope ratio was stronger in the snow addition treatment compared to the warming and nitrogen addition treatments (Figure 2).

### 3.3 | Trait Effects on Species Establishment

Out of the 131 plots included in this synthesis, at least one species was established in 97 of the plots during the study duration with an average of 1.6 new species establishing (maximum number of newly establishing species was six) in a plot during the study duration. There were few strong trait effects on the probability that a species was established in a plot during these experiments. There were no significant overall effects of traits, treatments or their interaction on establishment probability (Figure 3). However, there were a few traits that had slopes different from zero under some global change treatments. Species with higher SLA and height were more likely to establish in snow addition plots, species with higher LDMC were more likely to establish in warming plots and species with smaller leaves and lower leaf nitrogen were more likely to establish in nitrogen addition plots (Figure 3). Axis PC1 also influenced establishment, with higher values of PC1 increasing the probability of establishment in nitrogen addition plots and a significant trait by treatment interaction. This suggests that this nitrogen addition trend differs from the trend found in snow addition plots, where there was a tendency for species with lower PC1 scores to be more likely to establish (Figure S3).

### 3.4 | Changes in Community Weighted Means and Differences Between Abundance and Establishment Trends

There were significant changes over time in CWM values for several traits in control plots. These include decreasing chlorophyll content and increasing SLA, leaf N15 and height (Figure 4; Figure S9). These traits changed similarly in the experimental treatments but were exaggerated in snow addition plots and dampened in warming plots. Nitrogen addition plots showed changes in leaf nitrogen (decrease) and snow addition plots showed changes in leaf C13 (decrease) and leaf area (increase). In addition, many changes in community-weighted means in the treatments did

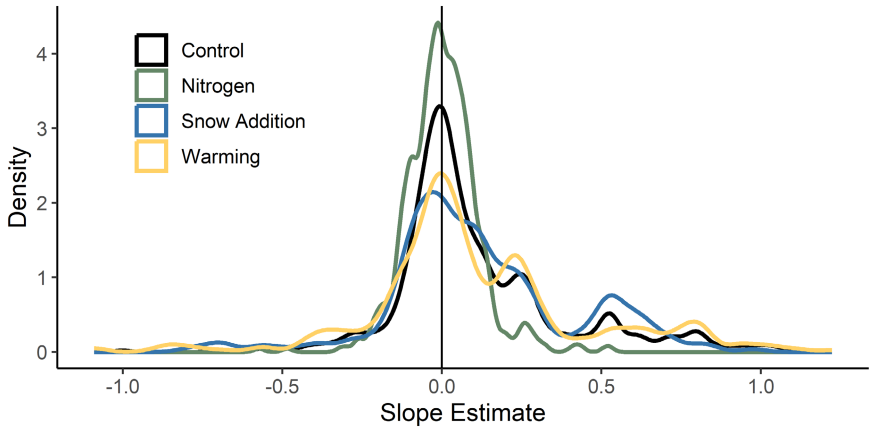


**FIGURE 1** | Density plot of species slopes (proportional abundance change per year) from six long-term (7–37 year) global change experiments across 70 species. These represent the linear slopes of change in abundance from a baseline abundance for each species in each plot of each experiment.

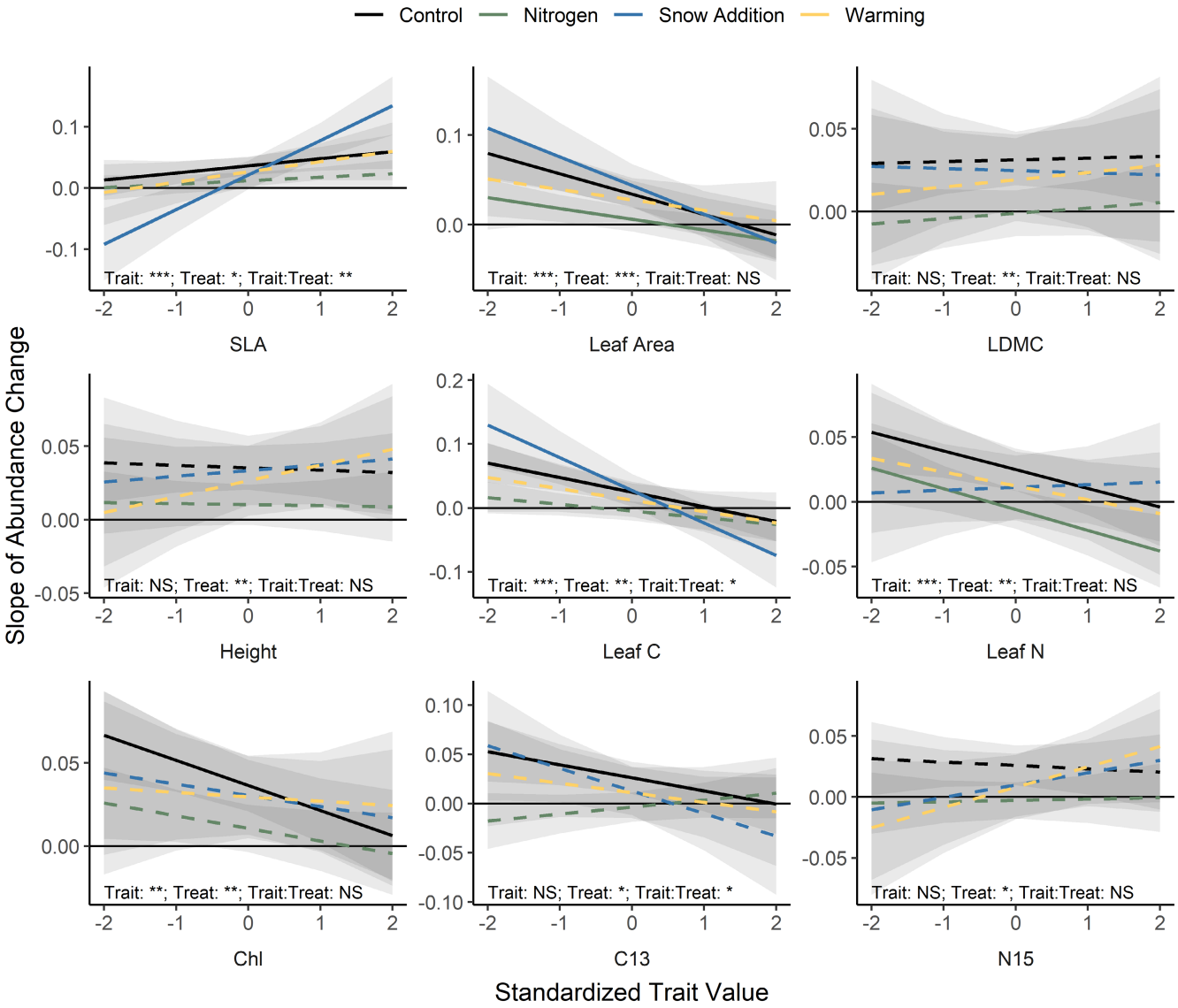


**FIGURE 2** | Modelled functional trait influences on change in plant abundance by global change treatment. Line colours indicate global change treatment type. Each trait was scaled and centred prior to analyses. Text indicates the significance of each model fixed effect where NS = $p > 0.05$, *$p < 0.05$, **$p < 0.01$ and ***$p < 0.001$. If the 'Trait' effect is significant, this indicates that there is an average trend across trait values where a species' abundance tends to increase at high or low trait values and decrease at the opposite end. A significant 'Treatment' effect indicates that plant abundance change differs between treatments on average, while the interaction effect indicates whether the trait-based slopes differ by treatment. Dashed lines indicate that the slope is not different from zero while solid lines indicate that zero is not included in the 95% confidence interval of the slope estimate. In the nitrogen-specific analysis, many traits had similar effects on species abundance change across all experiments. SLA, leaf area and leaf carbon showed different trends between experiments with the lowest effects observed in the N246 experiment, where the least nitrogen was added (Figure S4). See Figures S6 and S7 for plots with raw data and Table S1 for adjusted *p*-values.

not differ from changes observed in control plots, indicating that treatments did not have a different effect compared to background change during the study period for some traits. However, both nitrogen and snow addition had several changes that differed from control plots (Figure 4, triangle points).

Overall, there were differences between which traits had changes in CWMs and the traits that drove changes in the abundance and establishment of individual species (Figure 4). Notably, there were substantial increases in CWM height and N15 in all treatments except warming; however; height and N15 did not influence species abundance or establishment under the same treatments. Similarly, community-weighted mean LDMC increased in nitrogen addition plots while there was no LDMC effect on species abundance changes in these plots. Finally, there were consistent leaf area effects on species abundance trends where species with smaller leaves tended to increase in abundance in control, nitrogen addition and snow addition plots, a trend which was not reflected by changes in community weighted mean.

There were three species that had average dominance index values above 0.55 across all the experiments. These include the bunchgrass *Deschampsia cespitosa (L.) Beauv.* (Poaceae), the forb *Geum rossii* (R.Br.) Ser. (Rosaceae) and the sedge

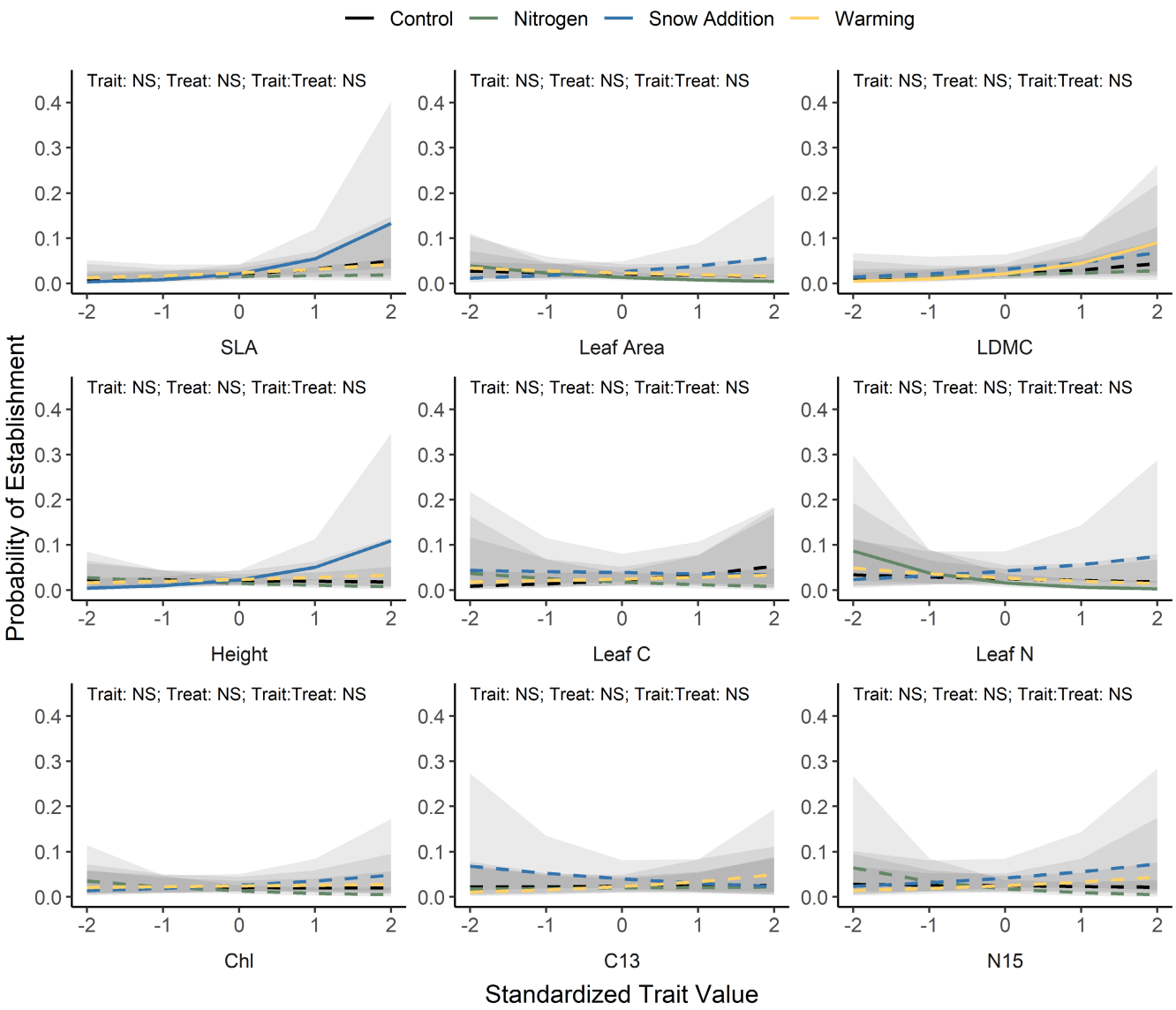


**FIGURE 3** | Modelled functional trait influences on plant establishment probability by global change treatment. Line colours indicate global change treatment type. Each trait was scaled and centred prior to analyses. Text indicates the significance of each model fixed effect where NS = $p > 0.05$, *$p < 0.05$, **$p < 0.01$ and ***$p < 0.001$. If the 'Trait' effect is significant, this indicates that there is an average trend across trait values where species are more likely to establish at high or low trait values and less likely to establish at the opposite end. A significant 'Treatment' effect indicates that plant establishment probability differs between treatments on average, while the interaction effect indicates whether the trait-based slopes differ by treatment. Dashed lines indicate that the slope is not different from zero while solid lines indicate that zero is not included in the 95% confidence interval of the slope estimate. See Figure S8 for plots that include raw data and Table S2 for adjusted *p*-values.

*Kobresia myosuroides* (Vill.) Fiori & Paol. (Cyperaceae, Figure 5). *Deschampsia cespitosa* and *G. rossii* were dominant in plots situated in wet or moist meadows while *K. myosuroides* was dominant in plots in dry meadows and thus did not co-occur with *D. cespitosa* or *G. rossii*. Overall, *D. cespitosa* increased consistently in all treatments except warming, while the other two dominant species most often decreased over time (Figure 5). The deviations between CWM trait responses and species-specific trait effects appear to be related to these dominant species responses. For example, *D. cespitosa* has relatively large height, LDMC and N15 content (Figure 5) relative to community average values, which increases CWM values of those traits even though these traits do not consistently affect species abundance or establishment probability (Figure 4). These deviations between CWM trends and species-specific trait effects are not as clear in the warming treatment, likely because dominant species showed little consistent responses to warming.

## 4 | Discussion

Our synthesis of six long-term global change experiments in the alpine tundra reveals that plant functional traits can mediate plant growth and establishment under global change and that global change is generating changes to community-weighted mean functional traits with likely consequences for ecosystem functioning. Generally, plants with more resource-acquisitive leaf traits, especially those with higher SLA or height, tended to increase under global change manipulations.

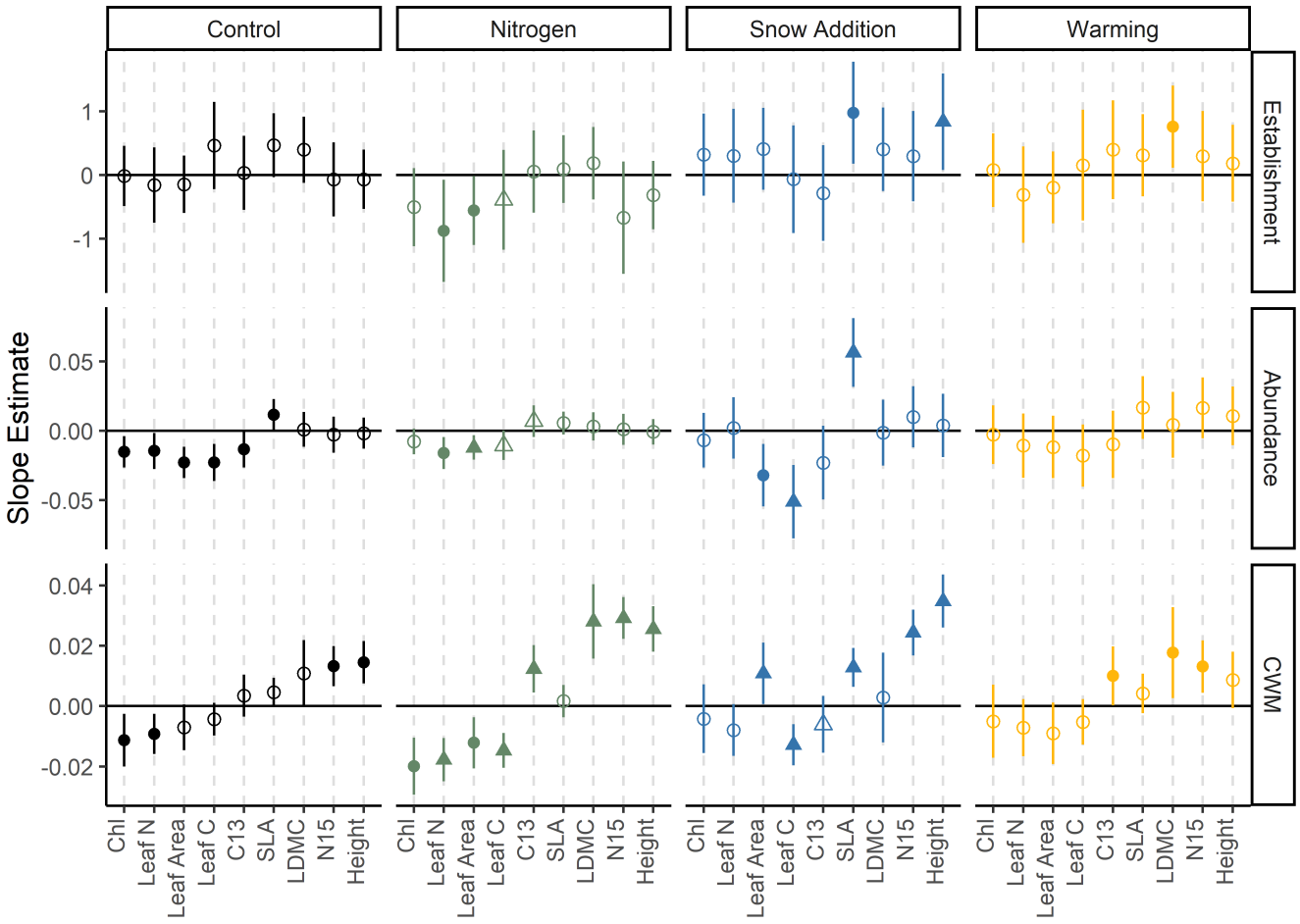


**FIGURE 4** | Comparison of trait effects on establishment probability and changes in abundance (as reported in Figures 2 and 3), along with community-weighted mean (CWM) trait responses across the global change treatments. Traits on the *x*-axis are arranged based on negative to positive CWM change in control plots. Solid points indicate where effects are different from zero (95% confidence interval does not overlap with zero), while triangles indicate a different effect than in the control plots (the effect in the control plots does not fall within the 95% confidence interval for the effect in the treatment plot). The results displayed here are from different models where abundance and establishment have species abundance log ratios and establishment as the dependent variable (results also reported in Figures 2 and 3) while CWM has the CWM as the dependent variable.

However, each global change factor also had different traits associated with abundance change or establishment probability. Additionally, while many traits were not related to individual species responses, there were strong trends in CWM changes. The deviations between CWM changes in height and N15 and species-specific trait effects on abundance and establishment suggest that changing abundances of dominant species can influence ecosystem functioning separately from average trait effects on species responses to global changes. By examining multiple facets of plant responses from species establishment and abundance change to community change under different global change factors, our synthesis reveals the multiple ways in which functional traits can play an important role in predicting ecosystem response to a variety of global changes.

### 4.1 | Species Are Responding to Ambient Change in Control Plots

While these experiments manipulated global change factors, the plants at this site have also experienced ambient changes in temperature, snow depth and nitrogen deposition, among other changes (Scharnagl, Johnson, and Ebert-May 2019; Williams et al. 2016). This is reflected in the changes seen in abundance, establishment and CWM trait values in control plots and is why we compare treatment effects to control effects over time. Thus, with long-term experiments, it is critical to consider that ambient conditions change while manipulations are occurring and in some cases, such changes can even exceed the strength of experimental changes (Langley et al. 2018). Here, ambient changes resulted in directional shifts in CWM in control plots towards generally more acquisitive communities that were taller, had higher SLA and had lower chlorophyll content, which is also reflected in the PC2 trend for control plots. The trend towards higher plant height matches previous findings in this system, but trends towards increasing SLA differ (Huxley and Spasojevic 2021; Oldfather et al. 2023), potentially due to differences in location and plant community type. For instance, dry meadows were abundant in Oldfather et al. (2023) but were less common at the experimental sites in this synthesis. In addition, Oldfather et al. (2023) found that *K. myosuroides* and *D. cespitosa*, common graminoids with relatively low SLA, showed large increases in abundance through time, but we found that *K. myosuroides* showed consistent decreases through time

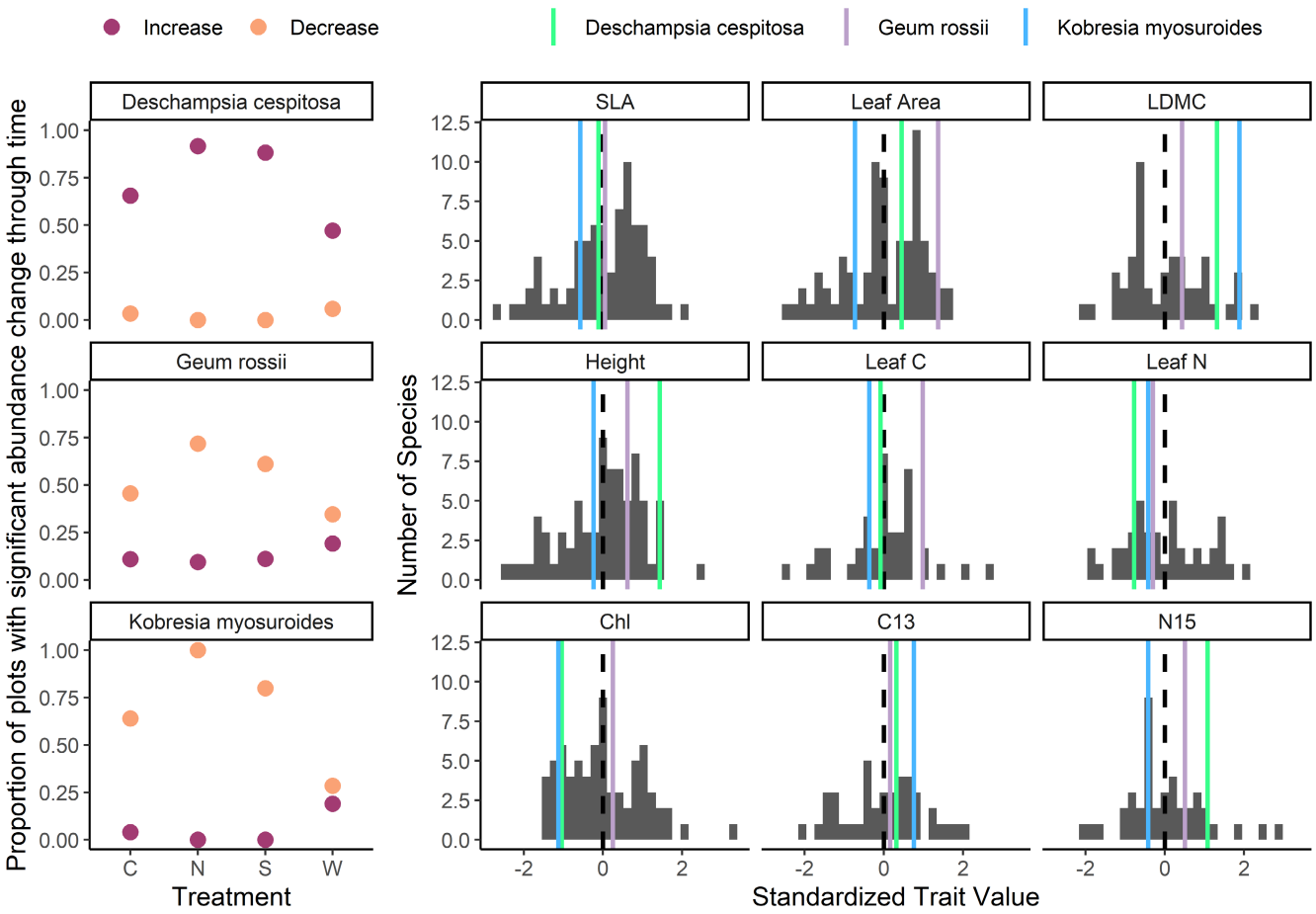


**FIGURE 5** | Dominant species responses to global change drivers and their traits relative to all species in the study. Panel (A) shows the proportion of plots where each dominant species showed significant positive (increasing) or negative (decreasing) abundance trends through time. Panel (B) shows the distribution of scaled and centred trait values for all species in dark grey. Dashed black lines indicate the zero line (average trait value of all species) and coloured lines indicate the position of the average trait value for each dominant species. Coloured lines to the right and left of the dashed line indicate that a dominant species had a higher and lower average trait value than the community average (i.e., all species), respectively.

across our experiments while *D. cespitosa* showed consistent increases (Figure 5). Increasing plant height is a trend also seen across the tundra more broadly including Arctic and alpine systems (Bjorkman et al. 2018; Jónsdóttir et al. 2023). However, the trend towards higher SLA was only seen in wet tundra communities globally (Bjorkman et al. 2018). Interestingly, there were no traits that were related to the chance of establishment in control plots, potentially because establishment events are rare in this system. There were also relatively few traits that showed effects on species abundance, establishment or CWM in experiment plots that differed from the effects in control plots, indicating that there are a few key traits (leaf nitrogen, leaf carbon, SLA) that might be most useful for predicting responses to global change. The traits that were important; however, differed between global change factors and between the change process (abundance vs. establishment vs. CWM change).

### 4.2 | Traits Related to Abundance Change Depend on Global Change Driver

Species abundance change reflects a combination of population and individual size change. Increases in abundance are a sign of successful survival, growth and/or reproduction and the relationship between traits and abundance change is an indication of the fitness contribution of traits. Overall, only a few key traits had significant effects on abundance change, but this is not surprising, as for a significant relationship to be detected, trait effects on abundance change would need to be relatively consistent across the 70 species occurring in our experiments for which we had trait data. Those traits that did influence abundance change across the treatments mostly aligned with our expectations. However, in nitrogen addition plots, species with lower leaf nitrogen or higher values of PC1 increased in abundance and establishment probability, potentially because these are the species that are weaker nitrogen competitors and thus benefit disproportionately under elevated nitrogen conditions (Kimball et al. 2016). This does not exactly follow our expectations that nitrogen addition should favour more acquisitive species (Zhou et al. 2018) and instead favoured more conservative species from a leaf nitrogen perspective. An increase in these lower-nitrogen species outweighed any potential increases in leaf nitrogen CWMs due to the nitrogen additions. This pattern is also a sign that legumes, whose nitrogen-fixing ability becomes less advantageous under increased nitrogen availability (Suding

et al. 2005), are suffering. Previous research shows that species in the alpine tundra are highly sensitive to nitrogen deposition (Bowman et al. 2006), likely because nitrogen is often the limiting nutrient in alpine soils and nitrogen cycling rates are low (Bowman et al. 1993; Burns 2004).

The snow addition treatment impacts on plant traits were in line with our expectations that acquisitive species should be favoured. Generally, species with cheaply constructed leaves (plants with higher SLA and lower leaf carbon content) increased in abundance. Snow addition experiments all occurred in moist meadow habitats that are adapted to snow cover for most of the year (Oldfather et al. 2023), but adding snow shortens an already short growing season, potentially favouring fast-growing species that can take advantage of the shorter growth window under additional snow. Results from an experiment at a higher elevation site with an even shorter growing season support this idea, with the fast-growing bunchgrass *D. cespitosa* outperforming the slower-growing forbs *Oxyria digyna* and *Silene acaulis* (Bueno de Mesquita et al. 2020). However, additional snow can also provide increased soil moisture during the growing season, potentially promoting increased productivity in forbs (Wipf and Rixen 2010). Snow addition showed the strongest trait-based responses, like other studies that also found strong functional trait responses to changing snow conditions in tundra (Huxley et al. 2023; Niittynen, Heikkinen, and Luoto 2020).

Finally, warming showed the weakest trait signals for changes in abundance, with no traits showing consistent directional effects on abundance change. This may be partially due to the relatively small influence of the open-top chambers that we used, as they tend to warm 1°C–2°C and only during the day during the growing season (Bokhorst et al. 2013). In addition, we did not account for non-vascular plants, which have been shown to have the strongest responses to experimental warming (Elmendorf, Henry, and Hollister 2012). Nevertheless, trends towards increasing SLA in warming experiments have been observed, especially in moist environments (Bjorkman et al. 2018; Wei et al. 2023). Furthermore, while none of our global change factors examined here involved increasing disturbance, research in grasslands has found that higher disturbance through grazing tends to favour more acquisitive strategies (Klumpp and Soussana 2009).

### 4.3 | Traits Affecting Species Establishment Are Different From Those Affecting Abundance Change

Species establishment in new areas is a critical factor in community responses to global change. The ability to establish will depend on different factors than the ability to survive and change in abundance. Thus, not surprisingly, our results showed that the traits that mattered for establishment were often, but not always, different from those that mattered for abundance change. In nitrogen addition plots, the traits related to the establishment were the same as those related to changes in abundance and should further solidify shifts towards species with lower leaf nitrogen and smaller leaves. On the other hand, the traits related to establishment differed from those related to abundance change for snow addition and warming plots. Most interestingly, species with higher leaf dry matter content were most likely to establish in warming treatments, the first sign that warming might favour more conservative species, as we expected. However, the establishment trends were generally quite weak and might indicate that global change factors only play a small role in influencing species establishment and that much of the observed changes in functional composition is due primarily to changes in species abundance, not species turnover. This could be expected, as tundra plants, both in general and at our field site, are overwhelmingly long lived, clonal perennials (Billings and Mooney 1968) though high levels of recruitment have been detected (Forbis 2003). Additionally, we did not include seed, dispersal or seedling traits in this analysis, which are likely more related to the ability to disperse and successfully establish in a new location (Larson and Funk 2016; Saatkamp et al. 2019) compared to the functional traits we measured. Future measurements and analyses of seed mass, vegetative reproduction, dispersal distances and other related traits would be very beneficial for better understanding the role that traits play in establishment dynamics. Nonetheless, these results show that traits are likely to vary in their effects on different community processes (Avolio et al. 2021) and that newly establishing species may be a sign of potential future changes in species composition.

### 4.4 | Dominant Species Responses Can Decouple Community Weighted Mean Change From Species-Specific Responses

Differences in trends between species-centred analyses (trait effects on establishment probability and abundance change) and trait CWM analyses also highlight how shifting perspectives between traits as characteristics that influence plant fitness versus traits as characteristics that generate ecosystem functions can reveal additional insights on the effects of global change at different scales (Lepš and de Bello 2023; Suding et al. 2008). Kandlikar, Kleinhesselink, and Kraft (2022) also found deviations between CWM change and species-specific trait effects on annual plant germination and fecundity but there are few studies that directly compare community and species-specific trait effects on responses to global change or the environment. Our study shows that these differences in patterns are often generated by how dominant species are responding to change and the trait values of these dominant species. This is likely because dominant species are often abundant across large environmental gradients and their responses to global change can be influenced by interactions with other subdominant species (Collins et al. 2022). The many observed directional changes in CWM trait values are likely to influence ecosystem functioning such as nutrient cycling and productivity (Hagan, Henn, and Osterman 2023; Huxley et al. 2023; Klumpp and Soussana 2009; Meier and Bowman 2008) as in our system, there is evidence that mass effects, rather than diversity, are the most important determinants of a variety of ecosystem functions (Huxley et al. 2023). For example, increasing snow depth is expected to result in higher productivity due to shifts towards communities with larger leaves, while decreasing snow depth is expected to result in lower productivity driven by a shift towards shorter communities with smaller leaves (Huxley et al. 2023).

## 4.5 | Study Limitations and Caveats

There are ways in which this approach could be improved. Global change factors are not changing in isolation (Komatsu et al. 2019) and examining interactions between global change factors is important for determining if non-additive responses are likely. There is also ample evidence that species can modify or adapt their phenotypes to changing conditions and that this process is key to species responses to change (Anderson and Song 2020; Henn et al. 2018). We were not able to include this intraspecific variation in our analyses, but devising methods of measuring traits of species exposed to these treatments through time will help to determine the limits to adaptation or phenotypic plasticity. We also do not examine seed traits potentially related to dispersal and seed establishment or belowground or clonal growth traits potentially related to resource acquisition or survival under different winter conditions. These suites of traits also likely affect species responses to these global change drivers and expanding measurements of these traits would enable more comprehensive analyses of trait-mediated plant responses to global change.

## 4.6 | Conclusions

This synthesis of experiments in an alpine system suggests several lessons for understanding how community-level traits respond to global change and how species-level traits influence species responses to global change across systems. First, it is useful to consider both the rate and magnitude of change for a given global change factor, as those factors with faster and/or more extreme changes should generate stronger and faster plant responses. This was potentially the case in our experiments, as the most subtle effects were the result of warming, potentially because the warming treatment imposed a more modest change compared to nitrogen or snow addition. However, it can be difficult to compare the magnitude of change across different global change drivers, as the effect of these changes will depend on plant sensitivity to the change and how extreme the changes are relative to some baseline value. Thus, low responsiveness to warming might also be due to a smaller direct effect of warming on plant communities compared to indirect effects on snow accumulation, growing season length or decomposition (Huxley et al. 2023). This is unlike reality for many Arctic and alpine regions where warming is happening very quickly. Second, when implementing long-term experiments, it is important to acknowledge that background conditions are changing and care should be taken to examine both observed effects of treatments and ambient change, as that change can be substantial (Langley et al. 2018). Third, our results suggest patterns that help to distinguish alternative outcomes of global change. For example, warming could favour more acquisitive species by relieving energy limitation, but this depends on moisture levels to support additional growth (Bjorkman et al. 2018; Moyes et al. 2015) and the traits that are related to success under warming suggest that our experimental sites may be somewhat moisture limited, as more conservative species with higher LDMC are more likely to establish in warming plots. Overall, this synthesis shows that functional traits are related to plant species responses to global change and the traits important to predicting responses depend on the global change factor in question. It also highlights how shifting perspectives from species-centred to community-centred responses can reveal different information about how ecosystems will respond to change.

### Author Contributions

M.J.S. and J.J.H. conceived of the idea and M.J.S. coordinated the working group. All authors participated in data preparation and honing research questions. J.J.H. led the analysis and writing of the manuscript. All authors provided feedback on the analysis and edited the manuscript.


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### Data Availability Statement

All data and code needed to compile the data and reproduce the analyses and figures in this manuscript are available at: doi.org/10.17605/OSF.IO/P9NXG and original datasets are archived at the Environmental Data Initiative and cited in the manuscript.

### Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14518.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section.