Received: 3 January 2022 | Revised: 31 January 2022 | Accepted: 17 May 2022

DOI: 10.1111/ele.14060

ECOLOGY LETTERS

LETTER

Global change re-structures alpine plant communities through interacting abiotic and biotic effects

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Funding information
Division of Environmental Biology, Grant/Award Number: 1637686, 2033292 and 2044006; Niwot Ridge LTER

Editor: Elsa Cleland

Abstract

Global change is altering patterns of community assembly, with net outcomes dependent on species' responses to the abiotic environment, both directly and mediated through biotic interactions. Here, we assess alpine plant community responses in a 15-year factorial nitrogen addition, warming and snow manipulation experiment. We used a dynamic competition model to estimate the density-dependent and -independent processes underlying changes in species-group abundances over time. Density-dependent shifts in competitive interactions drove long-term changes in abundance of species-groups under global change while counteracting environmental drivers limited the growth response of the dominant species through density-independent mechanisms. Furthermore, competitive interactions shifted with the environment, primarily with nitrogen and drove non-linear abundance responses across environmental gradients. Our results highlight that global change can either reshuffle species hierarchies or further favour already-dominant species; predicting which outcome will occur requires incorporating both density-dependent and -independent mechanisms and how they interact across multiple global change factors.

KEYWORDS

alpine, biotic interactions, competition, density-dependent, density-independent, dominance, global change, joint attribute modelling, plant communities, species hierarchies

INTRODUCTION

Global change is altering plant community dynamics, yet impacts are often difficult to predict and can vary across multiple, interacting drivers (Valladares et al., 2015). Understanding the net outcomes of global change on plant community structure is challenging because it requires integrating direct effects of changing environmental conditions (i.e. density-independent effects) with indirect effects of shifts in the magnitude and types of biotic interactions (i.e. density-dependent effects) (Götzenberger et al., 2012; Kraft & Ackerly, 2014; Vandvik et al., 2020). Community assembly theory has long recognised these biotic and abiotic 'filters' (HilleRisLambers et al., 2012; Kraft et al., 2015), however, more recent work emphasises that the impact of density-independent and -dependent processes cannot be separated (Cadotte & Tucker, 2017; Hallett et al., 2019). Rather, both contribute to species' persistence versus extinction risk (Germain et al., 2018; Pellissier et al., 2018) and temporal stability (Hallett et al., 2018), with cascading impacts on community composition and diversity.

Global change can cause complete restructuring of plant communities via density-dependent processes such as species turnover and/or reshuffling of competitive hierarchies (Brown et al., 1997; Dovrat et al., 2020; Smith et al., 2009). Alternatively, global change may further favour already-dominant species within a community, reducing species diversity via competitive exclusion or decreased evenness (Regina et al., 2018; Sheil, 2016). These dynamics can take years to play out, especially in long-lived and slow-growing systems, as short term responses may not fully encompass both environmental effects and shifts in biotic interactions (Komatsu et al., 2019). To meet these challenges, approaches that assess both density-independent and density-dependent mechanisms over long time periods are essential (Ehrlén & Morris, 2015).

Adding to this complexity, both the driver type (e.g. climate change, nutrient pollution, land use change) and number can have differential effects on plant community dynamics (Komatsu et al., 2019). Warming temperatures and altered precipitation regimes can shift species hierarchies through changes in competitive interactions under novel climate conditions (Hoover et al., 2014; Olsen et al., 2016; Valladares et al., 2015). This has been shown to reshuffle species dominance in field studies (Cavin et al., 2013; Evans et al., 2011; Mariotte et al., 2013), particularly in response to drought, given the well-established trade-off between competitive ability and stress tolerance (Gilman et al., 2010). On the other hand, nutrient pollution, such as atmospheric nitrogen deposition, is likely to reduce niche differentiation by homogenising habitats and may lead to competitive exclusion by dominant species (McKinney & Lockwood, 1999; Smart et al., 2006). Reduced species richness and increased production of one or a few species under nitrogen deposition is common, particularly in grassland ecosystems (Borge et al., 2004; Harpole et al., 2016; Zavaleta et al., 2003). In most natural systems, these different global change drivers occur simultaneously, and thus their net outcomes on community structure and the relative importance of density-independent versus density-dependent processes are often unclear.

While global change is altering plant community dynamics worldwide, alpine tundra ecosystems are particularly vulnerable, as elevation-dependent warming amplifies the rate of temperature increase in high versus low elevation systems (Pepin et al., 2015). Plant community transplant experiments in the Swiss alpine suggest increased temperature heightens extinction risk due to direct environmental effects along with novel species interactions and resulting changes in density-dependent processes (Nomoto & Alexander, 2021). Further, shifts in winter precipitation and snow pack along with atmospheric nutrient pollution from nearby urban and agricultural areas also pose a serious threat to the stability and diversity of alpine plant communities often finely adapted to local soil moisture and nutrient availability (Gobiet et al., 2014; Little et al., 2016; Roth et al., 2013). However, while there is high confidence that alpine regions will continue to warm at a rate faster than the global average (IPCC, 2018), predictions for changes in snow and nutrient pollution are much more uncertain, and vary considerably by region, latitude and land use history (Hock et al., 2019). Thus, correctly attributing changes in alpine tundra plant communities to warming temperatures, versus concomitant changes in snow and nutrient dynamics, is an ongoing challenge. What's more, how these interacting global change drivers influence both density-independent and density-dependent processes is an important knowledge gap in our understanding of rapidly shifting tundra plant communities.

Recent emphasis has been placed on understanding how dominant species within a community respond to global change, given their high abundances and disproportionate influence on ecosystem functions (Avolio et al., 2019; Hillebrand et al., 2018; Winfree et al., 2015; Wohlgemuth et al., 2016). Determining the mechanisms that allow species to dominate under novel environmental conditions can serve as proxies for whole community and ecosystem responses to global change (Avolio et al., 2019). In fact, the idea that "super-dominants," or overabundant populations of native species, may have similar impacts as non-native invasive species on community and ecosystem function has begun to gain traction (Regina et al., 2018; Zhao et al., 2021). Conversely, deciphering pathways by which dominant and subordinate species become more evenly distributed is critical for predicting the long-term maintenance of biodiversity and the preservation of rare species (Csergo et al., 2013; Felton & Smith, 2017). Broadly, viewing changes in plant community structure from an abundance-based rather than species or trait lens has shown to be a powerful way to make general predictions across systems (Suding et al., 2005).

Here, we present a 15-year fully factorial warming, snow manipulation and nitrogen (N) addition experiment with corresponding shifts in alpine plant community composition at Niwot Ridge, Colorado, USA. We estimate the influence of multiple global change drivers on the density-independent growth responses and density-dependent interactions of groups of dominant, subdominant, moderate and rare plant species over time using gjamTime, a dynamic, biophysical competition model (Clark et al., 2020). We use these model estimates to inform changes in the relative abundance of each species group observed in experimental field plots. Furthermore, we estimate the net effects of density-independent and -dependent factors on steady-state (i.e. equilibrium) abundances of each species group across both ambient and experimentally manipulated environmental gradients. We asked: (1) What global change scenarios lead to further favouring dominant species versus reordering species hierarchies? (2) How do density-independent and -dependent mechanisms influence the net outcomes of changes in plant community structure over time? (3) How do shifts in density-dependent interactions influence community stability under global change?

MATERIALS AND METHODS

Study design

The study site is a moist meadow habitat within the alpine tundra at Niwot Ridge Long Term Ecological Research (LTER) site in the Front Range of the Rocky Mountains, Colorado, USA (40°03'N, 105°35'W). The experimental design of this study is described in detail in Smith et al. (2012) and Farrer et al. (2014). Briefly, experimental plots (1 m^2) were established in 2006 with a fully factorial deployment of warming (using passive, open-top plexiglass chambers), N addition (using slow release fertiliser), and snow manipulation treatments (using snow fences) (see supplementary methods-experimental plots).

Our study focuses on warming, as this is the most consistent global change driver in alpine tundra ecosystems (Hock et al., 2019). While we assess community responses to all three global change drivers: warming, snow addition and N addition, we restrict our analysis to only the treatments that include experimental warming alone or in combination with snow and/or N addition (n = 40 plots). Thus, we compare the following four experimental treatments and contrast them to control (ambient): (1) warming only (W), (2) N addition and warming (NW), (3) snow addition and warming (SW) and (4) snow, N addition and warming (SNW). In addition to warming, altered snowpack is another crucial impact of global change in alpine ecosystems (Gobiet et al., 2014). While many regions, particularly at lower elevations and latitudes, are experiencing a decrease in snowpack with climate change, winter precipitation in the alpine at Niwot ridge has increased since the 1950s due to shifts in upper-air circulation patterns across the Continental Divide (Kittel et al., 2015). Finally, while atmospheric N emissions have decreased in many parts of the world, they are still increasing in highly developing areas and impacts on sensitive alpine ecosystems can be long-lasting with limited recovery of plant communities on decadal time scales (Bowman et al., 2018).

Plant community surveys

Plant community composition was measured in each plot annually from 2006 to 2020 during the peak of the growing season with pre-treatment data collected in 2006. A point-intercept method was used to estimate species presence at 100 points per plot in the field and these raw species counts were used in subsequent modelling with a censoring term of the total number of vegetative hits (i.e. excluding rock, litter, non-vascular species) in a plot in a given year (mean = 90). Thirty-three unique plant species were present in control plots across all years, however, we excluded species with <10 total observations (*n* = 13) to control for potential misidentification or recorder bias across similar species and congeners.

For our modelling approach (see below), we summed the cover data of our remaining 20 species into four species groups based on natural breaks in their relative abundance in control plots over time. First, the 'dominant' species, *Deschampsia cespitosa* (grass) had an average of 42 ± 1.2 (SE) plot hits (range: 20–67) in ambient conditions (control plots) forming a standalone group. Three 'subdominant' species were combined into one group: *Geum rossii* (forb), *Artemisia scopulorum* (forb) and *Carex scopulorum* (sedge) which had an average of 10 ±0.8 plot hits (range: 14–44) in ambient conditions. Four species were combined into one 'moderate' group: *Gentiana algida* (forb), *Trifolium parryi* (legume), *Bistorta bistortoides* (forb) and *Caltha leptosepala* (forb) which had an average of 3 ±0.3 plot hits (range: 3–29) in ambient conditions. Finally, we placed the remaining 12 species into one 'rare' group which had an average of 0.4 ±0.2 plot hits (range: 0–10) in ambient conditions (Figures S1 and S2).

We calculated changes in relative cover (plot hits) of each species group with respect to the pre-treatment (2006) data for each year over the 15-year period within each experimental treatment using the *abundance_change* function in the package codyn in R (Hallett et al., 2016). We then regressed these values using a linear mixed model with a fixed three-way interaction of species group, time (years since 2006) and treatment with a global intercept and a random effect of (calendar) year to determine whether each group increased, decreased or did not change in relative plot cover over the time period within a given treatment. Models were run using the *lmer* function in package lme4 in R (Bates et al., 2014; R Core Team, 2020). While the linear model best fit the overall dataset, some species groups showed non-linear changes in relative cover over time in certain treatments (see supplementary methods-modelling decisions and Table S4 for further information).

Generalised joint attribute modelling

Environmental covariates

We used a generalised joint attribute model to assess how density-dependent and -independent factors contribute to the observed changes in relative abundance of species groups over time and their steady-state predicted abundances across multiple global change drivers (Clark et al., 2020). We jointly estimated the influence of snow depth, nitrogen deposition and temperature on the density-independent growth rates of dominant, subdominant, moderate and rare species groups, with the above covariates used in each model. We incorporated continuous annual environmental data as model predictors, following the approach of Farrer et al. (2014) described below. Models were fit separately for each treatment combination across experimental and control plots, which allowed us to examine how environmental predictors alter the role of density-independent and -dependent factors under each global change treatment.

For temperature, we used local climate data measured daily at the nearby Niwot Saddle site (0.75 km away, 40°03'17"N, 105°35'21"W) from 2006 to 2019 via a Campbell Scientific CR23X data logger and measured in 10 min intervals (averaged to daily) in 2020 via a Campbell Scientific CR1000 data logger (Campbell Scientific Instruments, Logan, UT). We used the average summer temperature (June–August) of each year as the temperature value for control plots and then added 1°C to these values for warming plots (Figure S3). For Nitrogen deposition, we used background (atmospheric) deposition values from the National Atmospheric Deposition Program (NADP) database from the Niwot Saddle sensor (NTN site C002). Average summer values (June to August) of total N deposition ($NH_4 + NO_3$) for years 2006–2020 in g/m^2/year were used as the value for control and we added 14 g/m^2/year (2006–2010) or 5 g/m^2/year (2011–2020) to this value for N addition plots. Because of the ability of excess N to build up in the soil over time, we allowed 10% of the previous year's N pool to carry over to the following year in N addition plots creating a gradual increase in N availability over time (Figure S4). Finally, monthly snow depth (cm) measurements were taken in experimental plots at the block level (snow fence, control × 3) from 2009 to 2016 using metal snow poles. To infill additional years of study (2006–2008, 2017–2020) we regressed the measured values from experimental plots on monthly snow depth measurements from the same years at nearby Niwot Saddle plots (averaged across all plots) with treatment (snow fence/control) and experimental location (block) as additional model predictors ($R^2 = 0.742$, Pearson $r = 0.874$). We used mean April snow depth values for all years to reflect the snow accumulation prior to snow melt as a proxy for water availability at the start of the growing season (Figure S5) (see supplementary methods-environmental data and infilling for further details).

Model specifications

Joint responses of species groups to environmental predictors, interactions among species groups and the combination of these processes were estimated using the gjamTime model as described in Clark et al. (2020) via the R package gjam (Clark et al., 2017) with the gjamTime supplemental functions https://github.com/jimclarkatduke/gjam/blob/master/gjamTimeFunctions.R?raw=True.

Relative abundances of species groups were modelled as raw counts ('hits') of the a priori dominant, subdominant, moderate and rare species groups in each plot-year combination. Specifically, we used the 'DA' (discrete abundance) data type specification for count data, which accounts for both discrete counts and total effort (in our case defined as the total number of vegetative hits within the same plot-year [see Plant community surveys]). These response data are assumed to be censored, discrete realisations of a continuous latent vector (w_s) with a joint multivariate normal distribution with a mean of μ_s, which is a length *s* mean vector, and an error Σ, which is an *s* x *s* covariance matrix. In other words:

$$w_s \sim MVN\left(\mu_s, \sum\right) \tag{1}$$

Changes in population density of each species group over time are modelled using a Lotka-Volterra (LV) model specification from which the gjamTime model is derived:

$$\frac{dw_s}{dt} = \left(w_s \times X\right)\rho_s + \left(w_s \times w_{s'}\right)\alpha_s + \varepsilon_s \tag{2}$$

The first term defines the density-independent growth rate of a species group ($\rho_{s.}$) multiplied by the density of species group *s* and the environmental impact ($w_s \times X$). The second term defines the species-group's density-dependent growth rate $\alpha_{s,}$ which is modified by the density of two interacting species-groups s and s' ($w_s \times w_{s'}$). Finally, the last term encompasses residual species group error (ε_s) (Equation 2). (See supplementary methods, model fitting for further details).

We set model priors for α parameters to allow for negative (−1, 0) species group interactions (i.e. competition) only, as informed by previous work in this system (Farrer et al., 2014) (See supplementary methods-modelling decisions for further justification and discussion of potential facilitation). For ρ intercepts, we set wide model priors from (−1, 1) to allow for species groups to increase or decrease by a maximum of 100% of their cover in a given time step (1 year). We set priors on ρ coefficients as (−0.5, 0.5) to allow a 50% change (positive or negative) in ρ in response to a 1 SD change in a given environmental driver (standardised zero mean and unit variance) at each time step.

Finally, steady-state abundance distributions (w_s^*), that is, probabilistic predicted equilibrium abundances of species groups, were estimated by numerical integration of the modelled parameter estimates of environmental effects on density-independent growth rates and density-dependent interactions among species groups, allowing for interactive and non-linear responses to emerge across environmental gradients (i.e. Environment × Species interactions-ESIs, Clark et al., 2020). For each model output, we simulated 100 equilibrium abundance values for each species group at 10 discrete steps for each covariate across observed gradients of snow depth, N deposition and temperature, calculating a mean and standard deviation of the w_s^* estimates for each set of 100 simulations (see supplementary methods, model fitting for further details).

Model outputs

Models were run in a (state-space) hierarchical Bayesian framework, with model fitting by Markov chain Monte Carlo for 10,000 iterations with a burn-in period of 2000 using the function *gjam* in the package gjam in R (Clark et al., 2017; R Core Team, 2020). Model convergence was confirmed by visual assessment of the mixing of chains as well as model-fit diagnostic plots generated in the *gjamPlot* function of the gjam package (Figure S6(a–e)). We ran models separately for each of the four treatment types (W, NW, SW, SNW), as well as control (CTL). This allowed us to test the influence of global change drivers on density-independent growth rates and to compare estimated species interaction matrices between models of each global change treatment versus control; as the current gjamTime model does not test the influence of environmental covariates on density-dependent interactions directly.

The effects of standardised environmental drivers on density-independent growth rates (ρ_s) were assessed via the mean and 95% Bayesian credible intervals of parameter estimates. For density-dependent interactions of species groups (α_s), we calculated the difference in the mean estimates ($\alpha_{\mu s}$) between control plots and each global change treatment type for all species group pairs (i.e. $\Delta\alpha_\mu$). We then summed all changes in interspecific competition on a given species group and combined the interspecific and intraspecific $\Delta\alpha_\mu$ values to estimate the net change in competition on each species group within each treatment type. We discuss predicted steady-state distributions when one or more species groups showed non-linear patterns in equilibrium abundances over a given environmental gradient (see Clark et al., 2020).

Finally, to assess community stability, we used eigenvalue analysis from modelled interaction matrices; communities are considered stable if all real eigenvalues are negative (Allesina & Tang, 2012). We also compared the rightmost (highest) real eigenvalues to compare stability across communities whereby lower (more negative) rightmost real eigenvalues denoted higher stability (Carpentier et al., 2021).

RESULTS

Net outcomes: Changes in cover

Dominant increase

In all the global change treatments except for warming only (W), the dominant species, *Deschampsia cespitosa,* increased its relative cover compared to control plots, while subdominant and moderate species decreased their relative cover and rare species did not change. While most of the global change scenarios shared this pattern, the increase in dominance at the expense of subdominant and moderate species was the strongest in SNW plots, followed by the SW plots and then NW plots (Figure 1; Table 1). Furthermore, while the relative cover of the rare species group did not change across these treatments, some rare species experienced local extirpation from or recruitment into SNW, SW and NW plots over the experimental period (Figure S2).

Competitive reshuffling

The nature of community dynamics differed in the W global change treatment. Instead of increased dominance and a decline in evenness, species groups reshuffled in abundance whereby the dominant species declined in cover over time, while subdominant and rare species increased, and the cover of moderate species did not change (Figure 1; Table 1). Furthermore, this was the *only* experimental treatment where we observed a change in the relative abundance of the rare species group over time.

Ambient

We can contrast these two broad types of shifts in community structure under global change manipulations to the patterns observed under ambient conditions (CTL), which showed little directional change over time. The cover of dominant and subdominant species did not change, while the abundance of moderate species decreased and rare species slightly increased (marginally significant) (Figure 1; Table 1).

Density-independent processes

Dominant increase

In plots where dominance increased, environmental effects on density-independent growth rates were not always consistent with changes in species group abundance over time. For example, in the SNW plots, only the dominant species had a positive effect of added N, which is consistent with its increase over time (Figure 2; Table S1). However, subdominant and moderate species groups also strongly declined, suggesting that other density-dependent mechanisms were at play.

In SW plots, where we observed the second-highest increase in dominance, temperature and snow depth had counteracting (but weak) effects on *Deschampsia* growth rates. In contrast, snow addition and ambient N deposition increased subdominant growth rates while warming decreased subdominant and (to a lesser extent) moderate species growth rates (Figure 2; Table S1). For moderate species, the negative effects of warming in SW plots were

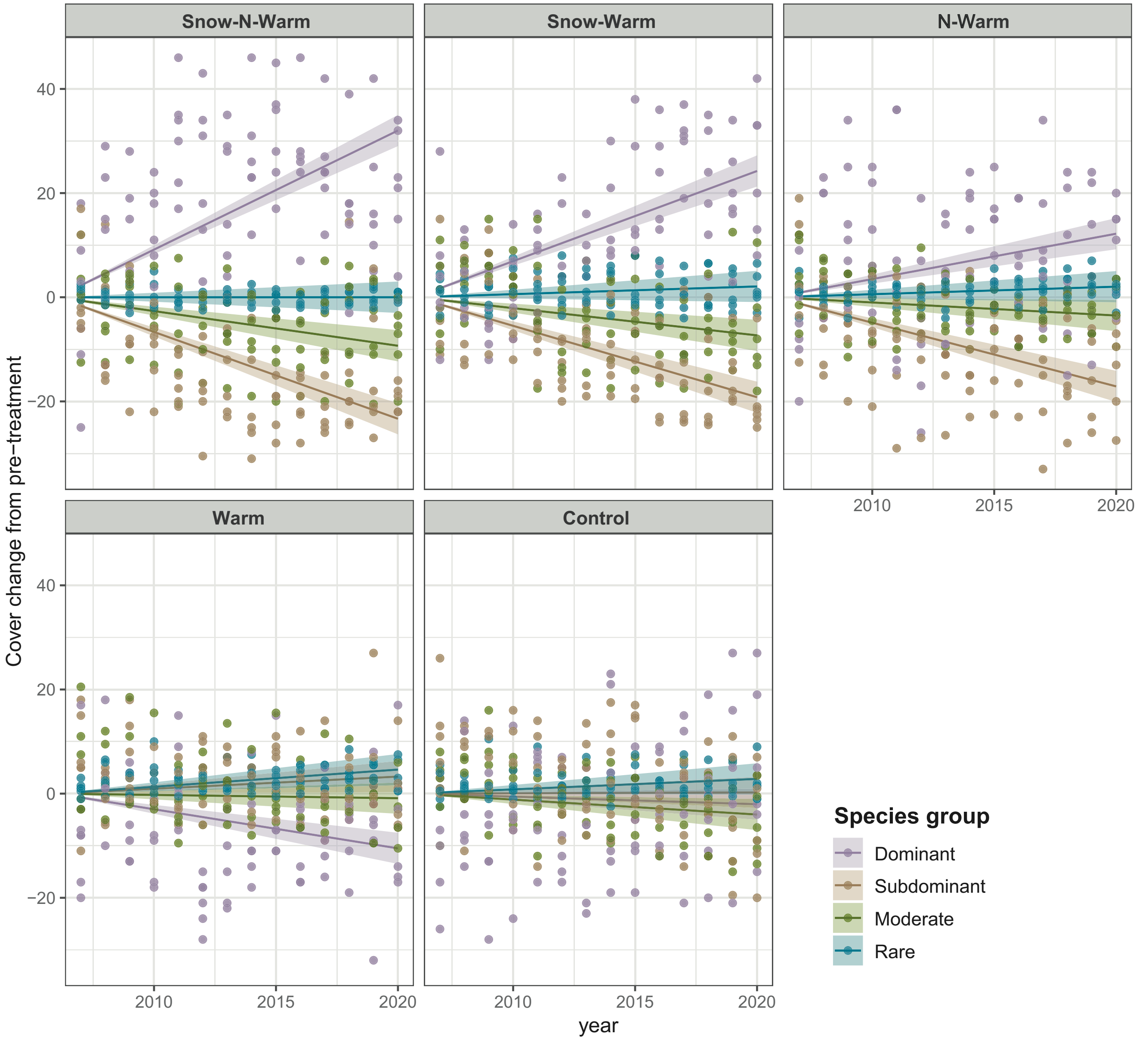

FIGURE 1 Net changes in cover. Changes in cover of species groups at the plot level with respect to pre-treatment values (2006) for each year (2007–2020). Points show the change in cover (i.e. 'hits') versus 2006 for a given plot by each species group within each year ($n = 6$ plots per treatment × 4 groups × 14 years). Lines reflect modelled estimates of cover change by treatment type, species group and duration of treatment (number of years since 2006) with a random effect of calendar year with 95% confidence intervals plotted around line estimates (Table 1).

consistent with their decline over time. However, counteracting (neutral) environmental effects on dominant and subdominant species do not explain their strong directional shifts in abundance.

In NW plots, where we observed the weakest increase in the dominant species, *Deschampsia* growth rates were positively influenced by N addition and strongly negatively influenced by warming (Figure 2; Table S1), suggesting that counteracting influences of nitrogen and warming muted the dominant increase over time. In addition, warming had a positive effect on the growth rates of moderate species, dampening the weaker negative effect of N addition, which may have reduced their magnitude of decline in these plots over time compared to other treatment types. However, subdominant species had no clear effects on the environment despite their decline in abundance.

Competitive reshuffling

In the W plots, where we observed species reshuffling, warming had no effects on density-independent growth rates. Instead, ambient snow depth had a positive effect on the dominant species growth rate and ambient N had a positive effect on subdominant and moderate species and a negative effect on the dominant species growth rates (Figure 2; Table S1). This supports the observed

TABLE 1 Changes in species group cover over time. Estimated lmer modelled slopes of changes in cover ('plot hits') of species groups with respect to pre-treatment (2006) cover per year over the 15-year period. Mixed models predicted the change in plot cover per year with a fixed interaction term of species group × treatment type x treatment duration (years since 2006) with a random intercept of calendar year and a global intercept of zero to determine if changes were positive or negative over time. P values were estimated using the package lmerTest in R (Kuznetsova et al., 2017) with 0.109 SE and 937.7 df for all species groups and treatments

Species group	Treatment	Estimate	*t* value	*p* value
Dominant	Snow + N + Warming	2.287	20.953	0.000
Subdominant	Snow + N + Warming	−1.667	−15.270	0.000
Moderate	Snow + N + Warming	−0.665	−6.096	0.000
Rare	Snow + N + Warming	0.000	0.002	0.998
Dominant	Snow + Warming	1.732	15.866	0.000
Subdominant	Snow + Warming	−1.371	−12.563	0.000
Moderate	Snow + Warming	−0.523	−4.790	0.000
Rare	Snow + Warming	0.148	1.358	0.175
Dominant	N + Warming	0.872	7.985	0.000
Subdominant	N + Warming	−1.223	−11.201	0.000
Moderate	N + Warming	−0.251	−2.296	0.022
Rare	N + Warming	0.145	1.328	0.185
Dominant	+Warming	−0.751	−6.876	0.000
Subdominant	+Warming	0.234	2.142	0.032
Moderate	+Warming	−0.062	−0.572	0.567
Rare	+Warming	0.330	3.020	0.003
Dominant	Control	−0.145	−1.327	0.185
Subdominant	Control	0.017	0.155	0.877
Moderate	Control	−0.287	−2.627	0.009
Rare	Control	0.202	1.850	0.065

pattern of community reshuffling in that subdominant and moderate species growth rates increased while contrasting positive and negative effects cancelled out any benefit of the environment for the dominant species. Rare species had no effect on environmental drivers in W plots despite their increase over time.

Ambient

In CTL plots where we observed weak or no directional changes over time, ambient snow depth had a negative effect on moderate species growth rates (Figure 2; Table S1), which may have influenced the decline in this species group over time. Ambient snow depth also had a positive effect on the dominant species growth rate (Figure 2; Table S1), yet no change was observed in the dominant species over time.

Density-dependent processes

Dominant increase

Models revealed several changes in species interactions consistent with observed declines in evenness. First, competitive effects on the dominant species declined in all plots where *Deschampsia* increased over time (SNW, SW and NW) (Figure 3; Table S3). In SNW and NW plots, this was driven primarily by reduced interspecific competition, while in SW plots this was driven primarily by reduced intraspecific competition of the dominant species on itself (Figure 3; Table S3). The dominant species increased its intraspecific competition in plots with added N (SNW, NW), consistent with the positive effect of N addition on its density-independent growth rates (Figure 2). Furthermore, net competitive effects increased in SNW and SW plots for subdominant and (to a lesser extent) moderate species, primarily driven by increased interspecific competition with each other, reflecting higher-order interactions that benefit the dominant species, and contribute to their decline in these treatments over time.

In the NW treatment, competitive effects declined for all species groups (except rare) (Figure 3; Table S3). Reduced competition, in combination with density-independent patterns observed, help explain the lower magnitude of moderate and subdominant species declines in NW compared to SW and SNW treatments. However, this pattern was more pronounced for moderate than subdominant species, likely due to a strong reduction in the competitive effect of the dominant on moderate species (Figure S8c). In addition, predictive steady-state distributions revealed a non-linear (left-skewed) distribution of subdominant species across the observed N gradient in NW plots, suggesting that subdominant species only benefit from competitive release at low N levels, after which the dominant takes over (Figure 4).

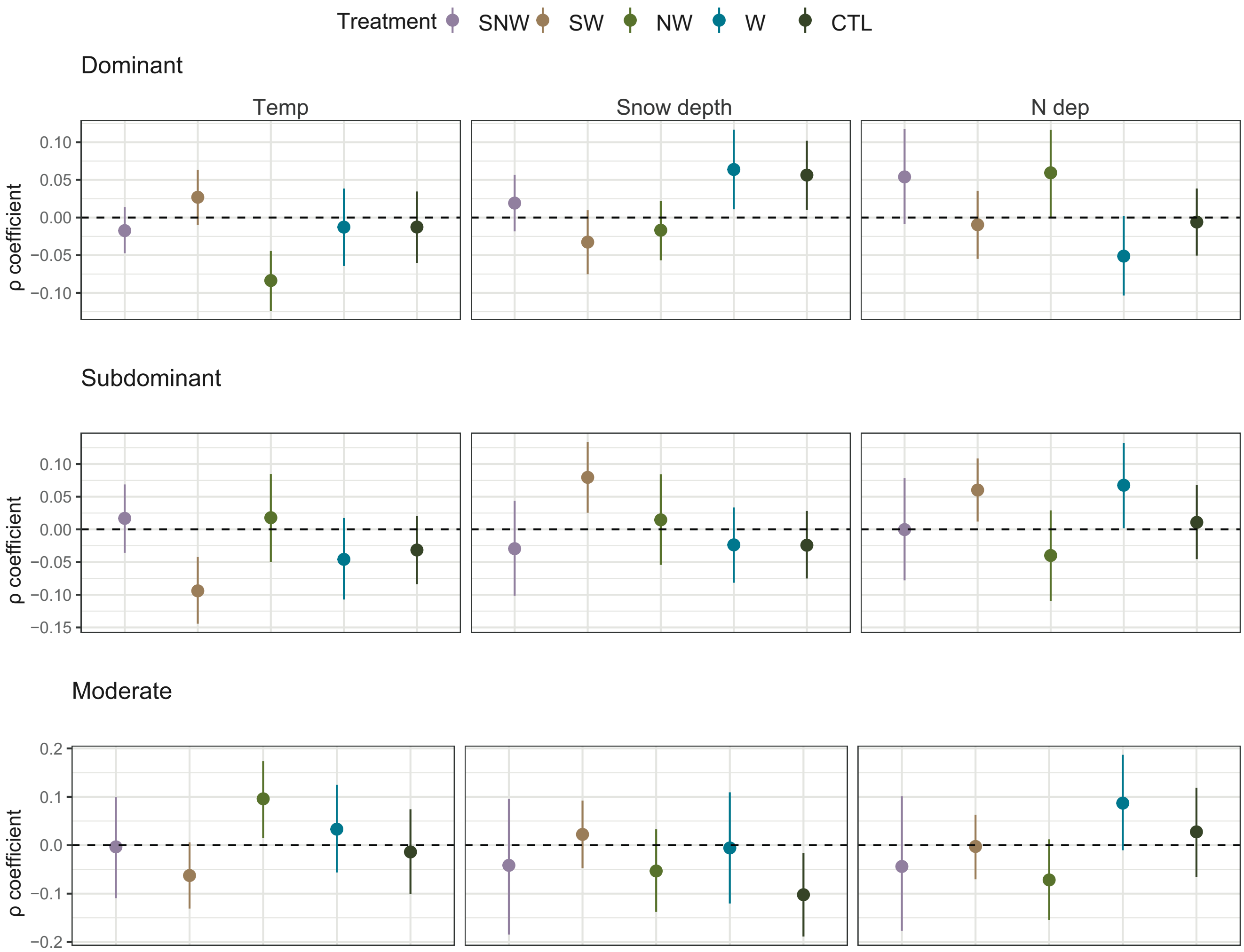

FIGURE 2 Density-independent mechanisms. Posterior parameter estimates for responses of density-independent growth rates (ρ_s) to standardised (mean 0 and unit variance) environmental covariates (temp-average summer air temperature (°C), snow depth-mean April snow depth (cm), N dep-average summer nitrogen deposition (g/m^2/year)). Points show mean estimates and error bars show 95% Bayesian credible intervals. We set wide priors on ρ coefficients (−0.5, 0.5) to allow a 50% change (increase or decrease) in ρ_s in response to a 1 SD change in a given environmental covariate at each time step. Estimates here reflect posterior sampling across all time steps. Estimates are standardised by environmental covariates within treatment as models were run separately for each treatment, thus the magnitude of parameter estimates and credible intervals should be compared between species groups *within* a treatment but not across treatments (colours). Rare species showed weak DI responses to environmental variables (Figure S7).

Competitive reshuffling

In W plots, where we observed species reshuffling, competitive effects strongly increased for the dominant species, mostly driven by the subdominant species group (Figure 3; Figure S8d; Table S3). This enhanced competitive pressure on the dominant species was not present in any other global change treatment (Figure 3; Table S3). Competitive effects also increased on the subdominant species, driven by enhanced competition from the moderate species group (Figure 3; Figure S8d; Table S3). Predictive steady-state distributions show that this was likely driven by competition for ambient N, as both moderate and subdominant species respond positively to ambient N in W plots (Figure 2). Thus at higher levels of ambient N, the subdominant species are outcompeted by the moderate species (Figure 4). Finally, net competition weakened slightly in W plots for rare species (Figure 3; Table S3), via reduced competition from the dominant species (Figure S8d), consistent with the increase of rare species in these plots over time.

Ambient

Intraspecific competition was high for dominant, subdominant and moderate species groups in CTL plots, indicating negative frequency dependence under ambient conditions (Table S2). There was also a relatively high competitive effect of moderate species on dominant species, while competition between dominant and subdominant, and moderate and subdominant species was relatively low, indicating niche partitioning between these groups (Table S2). Rare

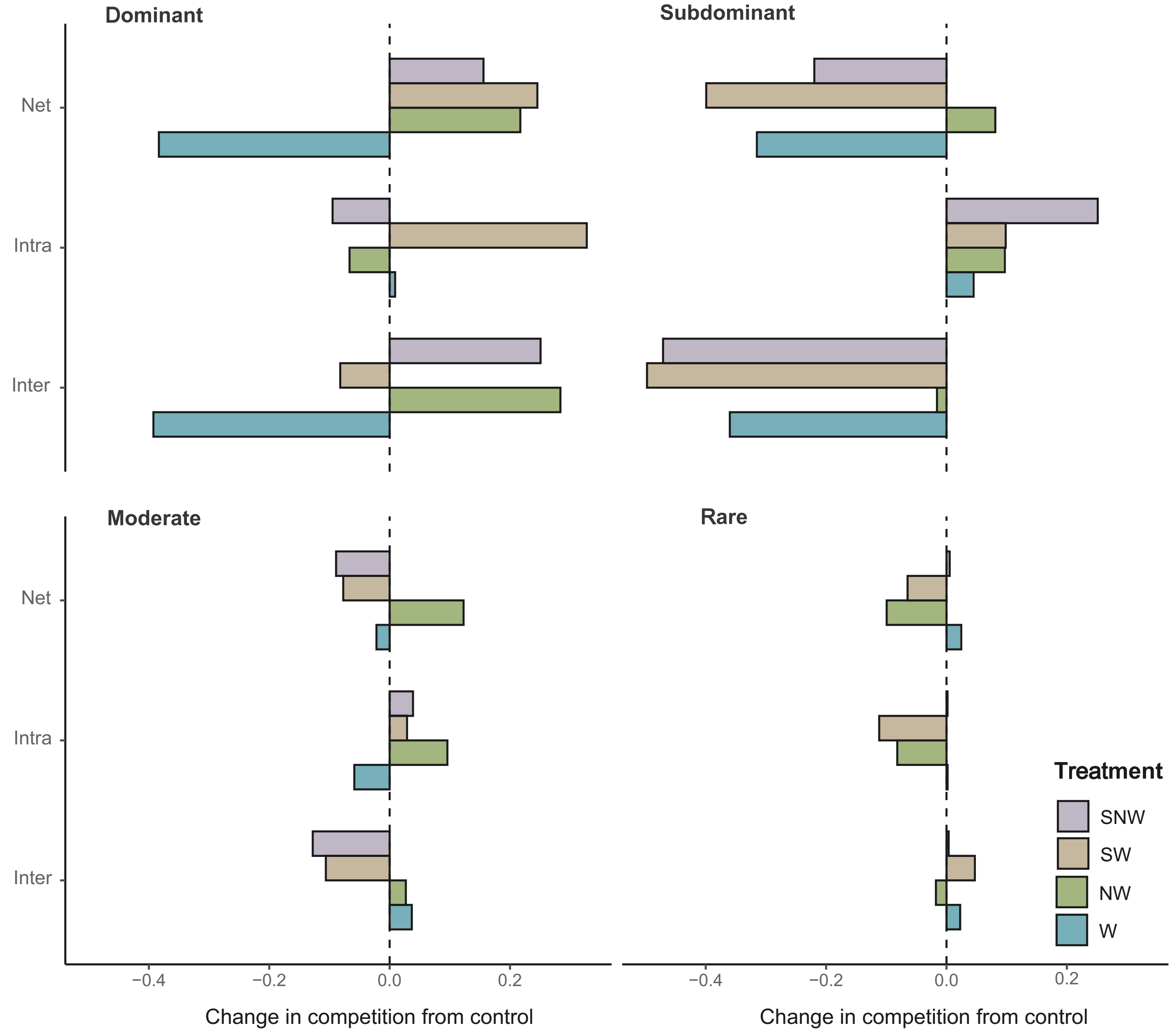

FIGURE 3 Density-dependent mechanisms. Changes in the mean competitive interactions ($\Delta\alpha_{\mu}$) of each species group in each global change treatment versus control. Intraspecific (intra) shows the mean change in the competition of a species group on itself (i.e. self-limitation). Interspecific (inter) shows the sum of the mean changes of all other species groups on that group. Net is the combination of intra and interspecific changes within each treatment and species group. Values to the left, right of the dotted zero line signify that competition on a species group became stronger, weaker in global change vs control conditions, respectively. Raw pairwise α and $\Delta\alpha_{\mu}$ values are shown in Tables S2, S3 and Figure S8(a-d).

species had neutral intraspecific and interspecific competition in as is expected due to low abundances (Table S2).

Community stability

Three out of four global change treatments (SNW, NW, W) and CTL communities were stable based on eigenvalue analysis, while SW communities were unstable (Table 2). Out of the stable communities, NW and W communities were more stable, while SNW communities were less stable than CTL, suggesting treatments with lower magnitude shifts in species group abundance are more stable over time.

The SW treatment was the only unstable community, likely due to a lack of self-limitation (intraspecific competition) of the dominant species (Table S2). Furthermore, the maximum equilibrium abundance of the dominant species is lower in SW versus other global change plots (Figure S9). Thus, the strong rate of increase over the last 15 years (Figure 1) suggests that the dominant species has likely overshot its carrying capacity in SW plots and will ultimately decline again, allowing the community to re-stabilise.

DISCUSSION

Global change is influencing plant community structure through shifts in species dominance and competitive hierarchies. Determining the co-occurring density-independent and -dependent mechanisms underlying these changes is critical to accurately predicting net outcomes for community structure and biodiversity maintenance over long time scales. Our study emphasises that density-independent processes cannot solely predict shifts in plant community composition under global change. Rather, global change also causes shifts in the degree of density dependence, through both direct effects on biotic interaction strengths and indirect effects of shifts in competitor abundances. While this

TABLE 2 Community stability eigenvalues. Real and imaginary coordinates of community eigenvalues from modelled interaction (α) matrices from gjamTime (Clark et al., 2020) for each treatment (plot type). The number of eigenvalues from each matrix is equal to the number of members in a community, here 4 species groups (dominant, subdominant, moderate and rare). Communities are considered stable if all real eigenvalues within that community are negative (Allesina & Tang, 2012). The rightmost real eigenvalue shows the highest (least negative/most positive) real eigenvalue within each treatment (i.e. community) whereby lower (more negative) rightmost real eigenvalues denote higher stability (Carpentier et al., 2021). Communities (treatment types) are ranked comparatively (4-highest stability to 1-lowest stability, 0-unstable)

Treatment	Real	Imaginary	Rightmost real	Stability	Stability rank (1–4)
Snow + N + Warming	−2.118	0.000	−0.008	Stable	1
Snow + N + Warming	−0.495	0.000	−0.008	Stable	1
Snow + N + Warming	−0.082	0.000	−0.008	Stable	1
Snow + N + Warming	−0.008	0.000	−0.008	Stable	1
Snow + Warming	−2.150	0.000	0.049	Unstable	0
Snow + Warming	−0.358	0.000	0.049	Unstable	0
Snow + Warming	−0.099	0.000	0.049	Unstable	0
Snow + Warming	0.049	0.000	0.049	Unstable	0
N + Warming	−1.994	0.000	−0.150	Stable	4
N + Warming	−0.561	0.000	−0.150	Stable	4
N + Warming	−0.150	0.148	−0.150	Stable	4
N + Warming	−0.150	−0.148	−0.150	Stable	4
+Warming	−2.223	0.000	−0.110	Stable	3
+Warming	−0.285	0.011	−0.110	Stable	3
+Warming	−0.285	−0.011	−0.110	Stable	3
+Warming	−0.110	0.000	−0.110	Stable	3
Control	−2.085	0.000	−0.072	Stable	2
Control	−0.575	0.000	−0.072	Stable	2
Control	−0.168	0.000	−0.072	Stable	2
Control	−0.072	0.000	−0.072	Stable	2

ultimately community instability in SW plots over time (Table 2).

Our approach of utilising species groups based on dominance rather than estimating species-specific patterns proved highly useful for predicting changes in community structure over time. Initial abundance rather than the functional mechanisms of a species were shown to be a strong predictor of species losses under atmospheric N deposition across ecosystem types (Suding et al., 2005). In addition, a recent study of plant responses to climate change in the Arctic tundra showed that rates of change in taxa over time were related to the baseline commonness of species early in the experiment (Post et al., 2021). Interestingly, we found very little change in the abundance of rare species over time despite shifts in competitive interactions and moderate effects of the environment on growth in some treatments (Figure 3; Figure S7). This may partially be due to species turnover within the treatment plots resulting from local extirpations and recruitment events of rare species over time (Figure S2). Thus, our results suggest that while individual rare species may be lost or gained under global change, the net abundance of rare species as a whole is maintained. However, what formally defines dominant vs rare species in a spatiotemporal setting is still somewhat elusive, and considering both the relative abundance and frequency of a species as well as its ecological impacts on the community is necessary (Avolio et al., 2019).

One functional strategy that provided insight outside of the abundance-based framework was the positive response of graminoids (grasses + sedges) to N addition. *D. cespitosa* growth responded positively to N addition (Figure 2), which is common for grasses due to belowground rhizosheath traits that allow for better N absorption while buffering against N-induced stressors (Tian et al., 2021, 2022). Although not modelled individually, a subdominant sedge (*Carex scopulorum*) also increased in cover over time in both SNW and NW plots, in contrast to the other two subdominant species (forbs) which declined in these treatments (Figure S2). Previous work in this system has also highlighted the high N growth response of *Carex* species (Bowman et al., 2006). However, accounting for the high N affinity of graminoids was not sufficient to predict changes in community structure over time, as weaker net competitive dynamics and counteracting negative effects of warming limited the net increase of the dominant species in NW plots (Figure 1).

Overall, our results provide a clearer understanding of how global change can lead to community reshuffling and varying degrees of diversity decline through reduced evenness of species groups, and that only considering density-independent responses to the environment fails to explain these different outcomes. It is well supported that direct (i.e. density-independent) species responses to the environment insufficiently predict how communities will be restructured under global change (Alexander et al., 2015; Liancourt et al., 2013; Suttle et al., 2007) but rather, depend on the interplay of density-independent and -dependent processes (Cadotte & Tucker, 2017; HilleRisLambers et al., 2012; Hallett et al., 2018). Yet many species distribution modelling (SDM) approaches continue to utilise only climatic or environmental constraints when predicting future species distributions (Davis et al., 1998; Roe et al., 2021; Swab et al., 2015). Our work suggests that this approach runs the risk of generating incorrect predictions, as density-dependent processes can yield ecological dynamics that vastly differ from direct environmental responses. Rather integrating community-level responses to multiple global change drivers through density-dependent and -independent mechanisms is critically needed for the maintenance of biodiversity (Avolio et al., 2021).

AUTHOR CONTRIBUTIONS

CGC, SCE and KNS designed the conceptual framework of the study including questions and broad approach. JGS and KNS established experimental plots and JGS led annual field data collection, compiled and organised the datasets for analysis. CGC ran statistical analyses, created manuscript figures and wrote the manuscript. SCE, LS, MS and MS provided guidance and feedback on statistical analyses and helped to draft the manuscript. All authors read, provided comments and approved the final manuscript.

ACKNOWLEDGEMENTS

We thank the following people for assistance with plot design, set up and data collection in the field: Isabel Ashton, Emily Farrer, Charlotte Riggs, Marko Spasojevic, Matt Khosh, Warren Sconniers, Kali Blevins, Beth McGarry, Bridget Hass, David Gonzalez, Krista Beckley, Eva Franzova, Sagar Yeraballi, Liana Nichols, Robert Weller, Adam Formica, Keishla Rodriguez, Shiyang Fu, Trang Pham, Robert Weller, Julia Reich, Liana Nichols, Jehane Semaha, Luke Tillmann, Pierre Mariotte, Joan Dudney, Riva Madan, Conor Bernard, Jared Huxley, Sam Sartwell, Caitlin White, Cliff Bueno de Mesquita, Kelsey Elwood, Josh Addison, AJ Lodge, Austin Willbern, Kenya Gates and Annika Rose-Person. This study was funded by the Niwot Ridge LTER (NSF DEB – 1637686). LGS and MCS were supported by NSF grant #2033292 and KNS acknowledges support from NSF grant #2044006.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.14060.

DATA AVAILABILITY STATEMENT

All data used in this study are available on the EDI Data Portal https://portal.edirepository.org/ and https://nadp.slh.wisc.edu/sites/ntn-CO02/ and the data DOIs are listed at the end of this article. All subsets of raw data and code needed to reproduce statistical analyses of this study are available on Github at https://github.com/cour10eygrace/NiwotITEX_gjam.

DATA DOIS

Plant community https://doi.org/10.6073/pasta/c771ce4b4eb9527b85bceb67c59b3bab

Snow depth https://doi.org/10.6073/pasta/8186d641539c37787495804b817e55ed

Air temperature https://doi.org/10.6073/pasta/846acb40f7e8a0491ee789428f4e4bea

Nitrogen deposition https://nadp.slh.wisc.edu/sites/ntn-CO02/

CODE DOI

Courtney Collins. (2022). cour10eygrace/NiwotITEX_gjam: release for Ecology Letters manuscript (1.00). Zenodo. https://doi.org/10.5281/zenodo.6599883

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SUPPORTING INFORMATION

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

How to cite this article: Collins, C.G., Elmendorf, S.C., Smith, J.G., Shoemaker, L., Szojka, M. & Swift, M. et al. (2022) Global change re-structures alpine plant communities through interacting abiotic and biotic effects. *Ecology Letters*, 25, 1813–1826. Available from: https://doi.org/10.1111/ele.14060