

Global change re-structures alpine plant communities under 15 years of warming, nitrogen, and snow addition: disentangling density independent and dependent effects

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Abstract

Global change is altering patterns of community assembly, with net outcomes dependent on species' responses to the 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. Density-independent processes were important when counteracting environmental drivers limited the growth response of the dominant species. Furthermore, competitive interactions shifted with environmental change, 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 favor 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.

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 local plant community structure is challenging because it requires integrating both direct effects of changing environmental conditions on individual species as well as shifts in the magnitude and types of biotic interactions (Götzenberger *et al.* 2012; Kraft & Ackerly 2014; Vandvik *et al.* 2020). Global change can cause complete restructuring of plant communities via species turnover and/or reshuffling of competitive hierarchies (Brown *et al.* 1997; Smith *et al.* 2009; Dovrat *et al.* 2020). Alternatively, global change may further favor already dominant species within a community, reducing species diversity via competitive exclusion or decreased evenness (Sheil 2016; Regina *et al.* 2018). 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.

Adding to this complexity, both the type (e.g. climate change, nutrient pollution, land use change) and the number of drivers can have differential effects on plant communities (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; Valladares *et al.* 2015). This has been shown to reshuffle species dominance in field studies (Evans *et al.* 2011; Cavin *et al.* 2013; Mariotte *et al.* 2013), particularly in response to drought, given the well-established trade-off between dominance 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 homogenizing 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 (Zavaleta *et al.* 2003; Borge *et al.* 2004). In most natural systems, these different global change drivers occur simultaneously, and thus their net outcomes on community structure are often unclear.

While global change is altering plant community dynamics worldwide, alpine tundra ecosystems are particularly vulnerable, as elevation dependent warming often amplifies the rate of temperature increase in high versus low elevation systems (Pepin *et al.* 2015). Additionally, shifts in winter precipitation and snow pack and 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 gradients of soil moisture and nutrients (Roth *et al.* 2013; Gobiet *et al.* 2014; Little *et al.* 2016). 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 co-occurring 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 (Winfree *et al.* 2015; Wohlgemuth *et al.* 2016; Hillebrand *et al.* 2018; Avolio *et al.* 2019). 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 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 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 (ie. equilibrium) abundances of each species group across both ambient and experimentally manipulated environmental gradients. We asked: 1) What global change scenarios lead to further favoring 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 density-dependent shifts 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, 105deg35' W). The experimental design of this study is described in detail in Smith *et al.* (2012) and Farrer *et al.* (2014). Briefly, experimental plots (1m²) were established in 2006 with a fully factorial deployment of warming (using passive, open-top plexiglass chambers), nitrogen (N) addition (using slow release fertilizer), and snow manipulation treatments (using snow fences) (See supplementary methods).

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 analyses to only the treatments that include experimental warming either alone or in combination with snow and N addition (n=40 plots). Thus, we compare the following four experimental treatments and contrast them to full control (ambient conditions): 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 2006-2020 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 modeling 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 only included species (n=20) with at least total 20 observations in control plots across all years.

For our modeling approach (see below), we summed the cover data of these 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 (Fig S1). Raw cover of all species over time in all treatment and control plots are shown in Fig S2.

We calculated changes in relative cover (plot hits) of each species group (Dominant, Subdominant, Moderate, and Rare) with respect to the pretreatment (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 modeled these values using a linear mixed model with a fixed 3-way interaction and a global intercept (0+ time (years since 2006) x species group x treatment) and a random intercept 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).

Generalized joint attribute modeling

Environmental predictors

We used a generalized joint attribute model for dynamic data (below) 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 both in experimentally manipulated and control plots over time. We incorporated continuous annual environmental data as model predictors, following the approach of Farrer *et al.* (2014), as environmental data were not available at the plot level for the entirety of the study (See supplementary methods).

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 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 modeled as raw counts ('hits') of the *a priori* dominant, subdominant, moderate and rare species groups in each plot-year combination censored by the total number of vegetative hits within the same plot-year with a maximum of 100 hits per plot (see Plant community surveys). This censoring value reflects the observation effort term as described in Clark *et al.* (2020) and we used the 'DA' (discrete abundance) data type specification for count data. Censored response data are then stored as a 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 $s \times s$ covariance matrix. In other words:

$$w_s \sim MVN(\mu_s, \Sigma) \text{ (eq. 1)}$$

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

$$\frac{dw_s}{dt} = (w_s \times X)\rho_s + (w_s \times w_{s'})\alpha_s + \varepsilon_s \text{ (eq. 2)}$$

The first term defines the density-independent growth rate of a species group (ρ_s) multiplied by the density of species groups and the environmental impact ($w_s \times X$). The second term defines the species-group's density-dependent growth rate α_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) (eq. 2).

Because this is a community of functionally similar herbaceous plant species competing for limited resources during a short growing season, we set model priors for α parameters to allow for negative (-1, 0) species group interactions (i.e. competition) only. 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 given environmental driver at each time step.

Equation 2 is then reorganized as the discrete-time version of the LV model (eq 2.1) for model fitting:

$$\Delta w_{st} = P'v_{st} + A u_{st} + \Sigma^{1/2}\varepsilon_{st} \text{ (eq. 2.1)}$$

where Δw_{st} is the growth increment for population abundances of s species group, P and A are sparse matrices which reorganize ρ and α coefficients respectively to optimize posterior simulation and allow for direct sampling (see Clark *et al.* 2020 SI Appendix S2.9, 2.10), v_{st} is a length- V vector where V is a block matrix of all possible combinations of species abundances w_{st} and q environmental variables ($w_{st} \times X_{qt}$), u_{st} is a length- U vector where U is a block matrix of all possible combinations of species group interactions ($w_{st} \times w_{s't}$), ε_{st} is a random vector and $\Sigma^{1/2}$ is a square root matrix for the $s \times s$ process error covariance.

Finally, steady-state abundance distributions, i.e. probabilistic predicted equilibrium abundances of species groups, were estimated by numerical integration of the modeled parameter estimates of environmental effects on growth rates and interactions among species groups allowing for interactive and non-linear responses to

emerge across environmental gradients (i.e. Environment x Species interactions- ESIs, Clark et al 2020). For each model output, we simulated 100 equilibrium abundance values for each species group at 10^3 discrete steps (10 steps for each covariate x covariate combination) 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).

We chose to run models at the species group level (dominant, subdominant, moderate and rare) rather than at the individual species level to improve model predictions and to address broad questions about shifts in community structure under global change. This species-group approach captures rare species' joint contribution to community dynamics in a biologically meaningful way, and allows for conceptual comparisons across multiple global change scenarios that would be too complex using the entire species set ($n=20$). The species-grouping model also better predicts the data (Fig S1), in particular for species with moderate and rare coverage, thus increasing parameter estimate confidence.

Model outputs

Models were run in a (state-space) hierarchical Bayesian framework, with model fitting by Markov chain Monte Carlo for 10000 iterations with a burn-in period of 2000 using the function 'gjam' in the package gjam (Clark *et al.* 2017). 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 (Fig S6 a-e). We ran models separately for each of the four treatment types (W, NW, SW, SNW), as well as the control (CTL), to compare the influence of global change drivers on growth rates and biotic interactions over time. Because the current gjamTime model does not test the influence of environmental covariates on density-dependent interactions, we ran a separate gjamTime model for each treatment type and then compared estimated species interaction matrices between models of each global change treatment versus control plots.

The effects of 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 (α_u) between control plots and each global change treatment type for all species group pairs (i.e. $\Delta\alpha_s$). We then summed all changes in interspecific competition on a given species group and combined the interspecific and intraspecific $\Delta\alpha_s$ 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 modeled 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

Fifteen years of experimental manipulations resulted in distinct changes in community structure based on the patterns of relative cover change in species groups. Most often, global change treatments led to an increase of the already dominant species within the community (i.e. 'Dominant increase'), while in one scenario global change lead to the reshuffling of species hierarchies (i.e. 'Competitive reshuffling'). In contrast, in ambient conditions (CTL), net changes strongly overlapped across species groups and were highly variable between years, indicating little directional change over time. We describe each outcome below.

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 (Fig 1, Table 1).

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 (Fig 1, Table 1). Furthermore, this was the *only* 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) (Fig 1, Table 1). Given that different global change treatments resulted in distinct shifts in community structure, we then ask whether density-independent responses to the environment or density-dependent species interactions best explain these shifts.

Density independent processes

All three environmental drivers (snow, N, and temperature) influenced the density-independent growth rates of species groups with varying consistency and magnitude across treatments (Fig 2, Table S1). Drivers often had counteracting effects, reducing the benefits of enhanced resource availability (water, N, and temperature) on density-independent growth rates. In addition, rare species had very few responses to environmental drivers (Fig S7), consistent with the limited change in cover of this group over time.

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 (Fig 2, Table S1). However, in SNW plots, subdominant and moderate species groups also strongly decline, suggesting that other density-dependent mechanisms are 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 (Fig 2, Table S1). For moderate species, the negative effects of warming in SW plots were 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 (Fig 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 of 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 (Fig 2, Table S1). This supports the observed 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 of environmental drivers in W plots despite their increase over time (Fig S7).

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 (Fig 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 (Fig 2, Table S1), yet no change was observed in the dominant species over time.

Density dependent processes

Incorporating density-dependent shifts in competitive interactions more fully explained the directional changes in species group cover over time (Fig 3, Table S2, S3). Broadly, global change treatments shifted intraspecific and interspecific competition in ways that reduced net competition for the dominant species but increased net competition for subdominant and to a lesser extent, moderate and rare species (Fig 3, S8). The major exception to this pattern was in the W plots, where we observed an increase in net competition for the dominant species. In addition, density-dependent species interactions shifted along environmental gradients, primarily N, leading to non-linear abundance distributions for subdominant species.

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) (Fig 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 (Fig 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 (Fig 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) (Fig 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 (Fig 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 benefits from competitive release at low N levels, after which the dominant takes over (Fig 4).

Competitive reshuffling

In W plots, where we observed competitive reshuffling, competitive effects strongly increased for the dominant species, mostly driven by the subdominant species group (Fig 3, S8, Table S3). This enhanced competitive pressure on the dominant species was not present in any other global change treatment (Fig 3, Table S3). Competitive effects also increased on the subdominant species, driven by enhanced competition from the moderate species group (Fig 3, S8, , 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 (Fig 2). Thus at higher levels of ambient N, the subdominant species are outcompeted by the moderate species (Fig 4). Finally, net competition weakened slightly in W plots for rare species (Fig 3, Table S3), via reduced competition from the dominant species (Fig S8), 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, Fig S8). 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, Fig S8). Rare species had neutral intraspecific and interspecific competition in as is expected due to low abundances (Table S2, Fig S8).

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). We can further see this in that the maximum equilibrium abundance of the dominant species is lower in SW versus other global change plots (Fig S9). Thus, the strong rate of increase over the last 15 years suggests that the dominant species has likely overshot its carrying capacity in SW plots and will ultimately decline again to regain community stability.

Discussion

Global change is influencing plant community structure by leading to shifts in species dominance and competitive hierarchies. Determining the co-occurring density-independent and dependent mechanisms underlying these changes is critical to accurately predict net outcomes for community structure and biodiversity maintenance over long time scales. While this concept is not new to community ecology, few studies (to our knowledge) have fully parameterized the density-dependent and independent components of species changes over long time scales under multiple scenarios of global change.

Our work highlights the importance of density-dependent mechanisms, including shifts in intra- and inter-specific competitive strengths, in driving long-term changes in the abundance of species groups under global change. We show that these competitive interactions can shift with the environment, in our system primarily with N, and drive non-linear species responses across environmental gradients further influencing community structure. Furthermore, despite significant shifts in community structure under global change, community stability can persist, or even increase, given that the dominant species maintains negative density-dependence.

Overall, our results provide a clearer understanding of how global change can lead to either 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 or only partially explains these outcomes. It is well supported that that direct (i.e. density-independent) species responses to the environment insufficiently predict how communities will be restructured under global change (Suttle *et al.* 2007; Liancourt *et al.* 2013; Alexander *et al.* 2015). Yet many species distribution modeling (SDM) approaches continue to utilize only climatic or environmental constraints when predicting future species distributions (Davis *et al.* 1998; Swab *et al.* 2015; Roe *et al.* 2021). Our work suggests that while this approach may inform changes for some species groups under certain global change scenarios, such as dominant species responses to N, it is limited in understanding community-level responses to multiple global change drivers, which is critically needed for the maintenance of biodiversity (CITE).

Finally, our approach of utilizing 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 suggest that commonness itself may be a strong predictor of response types, as rates of change in taxa over time were related to the baseline commonness

of species early in the experiment (Post *et al.* 2021). Rarity and dominance within a community are only informative at local to regional scales; these designations are based on the species pool in which the species exists, as well as the mechanisms driving its local dominance vs. rarity, making global scaling difficult. In addition, 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 critical (Avolio *et al.* 2019). Despite these caveats, understanding how and why patterns of dominance will shift with global change is of critical importance for predicting novel community assemblages and corresponding changes in community diversity and stability.

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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/>

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Fig. 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 x 4 groups x 14 years). Lines reflect modeled 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).

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Fig. 2 Density Independent mechanisms. Posterior parameter estimates for responses of density-independent growth rates (ρ_s) to standardized environmental covariates (Temp-average summer air temperature (°C), Snow depth-mean April snow depth (cm), N dep-average summer nitrogen deposition (g/m²/yr). 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 given environmental covariate at each time step and estimates here reflect posterior sampling across all time steps. Rare species showed weak DI responses to environmental variables (Fig S7). Estimates are standardized by 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 (colors).

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Fig. 3 Density Dependent mechanisms. Changes in the mean competitive interactions ($\Delta\alpha$ s) of each species group in each global change treatment versus control. Intraspecific (Intra) shows the mean change in 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 that competition on a species group became stronger, weaker in global change vs control conditions respectively. Raw pairwise α and $\Delta\alpha$ values shown in Tables S2, S3, and Fig S8 (a-d).

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Fig. 4 Competitive interactions drive non-linear responses to ambient and added N. Estimated steady-state abundance distributions (relative plot proportions) for each species group across the observed gradients of ambient (left) and added (right) N deposition (zero centered +/- two standard deviations) in NW and W global change plots (See Fig S9 for all treatments). Points show simulated equilibrium abundances (100 at each value of x). Dotted lines show best model fit from a general additive model in the *geom_smooth* function in ggplot2 (Wickham 2009)..

Table 1. Changes in species group cover over time

Estimated lmer modeled 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 x 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.

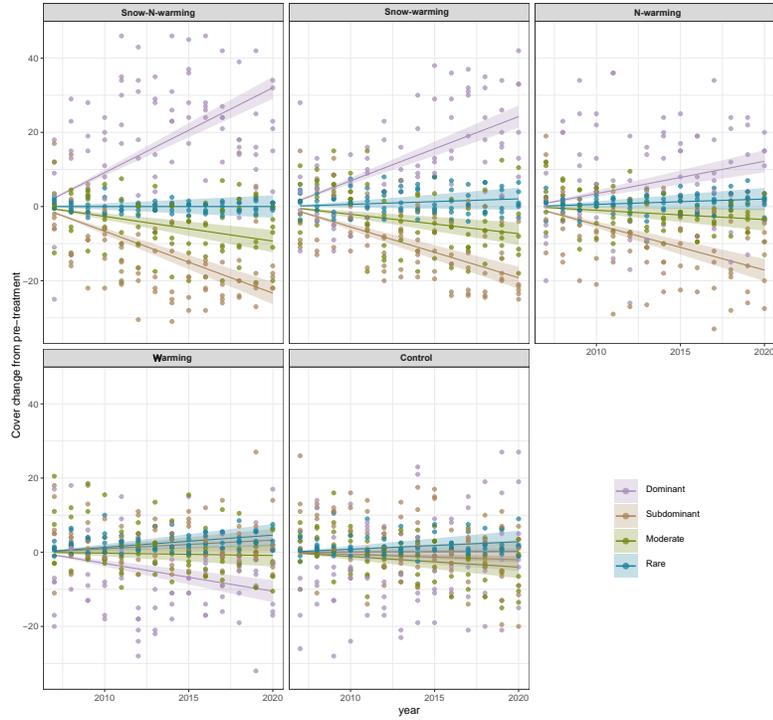
Species group	Treatment	Estimate	t value	P value
Dominant	Snow + N + Warming	2.287	20.953	0.000
Subdominant	Snow + N + Warming	-1.667	-15.270	0.000
Moderate	Snow + N + Warming	-0.665	-6.096	0.000
Rare	Snow + N + Warming	0.000	0.002	0.998
Dominant	Snow + Warming	1.732	15.866	0.000
Subdominant	Snow + Warming	-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

Species group	Treatment	Estimate	t value	P value
Rare	Control	0.202	1.850	0.065

Table 2. Community stability eigenvalues

Real and imaginary coordinates of community eigenvalues from modeled interaction (α) matrices from gjam-Time (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).

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



Treatment SNW SW NW W CTL

