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Mammalian herbivory shapes intraspecific trait responses to warmer climate and nutrient enrichment

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Abstract

Variation in intraspecific traits is one important mechanism that can allow plant species to respond to global changes. Understanding plant trait responses to environmental changes such as grazing patterns, nutrient enrichment and climate warming is, thus, essential for predicting the composition of future plant communities. We measured traits of eight common tundra species in a fully factorial field experiment with mammalian herbivore exclusion, fertilization, and passive warming, and assessed how trait responsiveness to the treatments was associated with abundance changes in those treatments. Herbivory exhibited the strongest impact on traits. Exclusion of herbivores increased vegetative plant height by 50% and specific leaf area (SLA) by 19%, and decreased foliar C:N by 11%; fertilization and warming also increased height and SLA but to a smaller extent. Herbivory also modulated intraspecific height, SLA and foliar C:N responses to fertilization and warming, and these interactions were species-specific. Furthermore, herbivory affected how trait change translated into relative abundance change: increased height under warming and fertilization was more positively related to abundance change inside fences than in grazed plots. Our findings highlight the key role of mammalian herbivory when assessing intraspecific trait change in tundra and its consequences for plant performance under global changes.

KEYWORDS

anthropogenic change, climate warming, grazing, herbivory, intraspecific trait plasticity, nutrient addition, open-top chamber, plant performance, reindeer, trait–environment relationship

1 | INTRODUCTION

Around the globe, high latitude and altitude systems face shifts in grazing regimes concurrently with increasing temperatures and accelerated nutrient cycling (Aerts, 2006; Uboni et al., 2016; Wookey et al., 2009). Recent studies have successfully predicted

community responses to these anthropogenic changes using species' functional traits (i.e. interspecific traits; Bjorkman et al., 2018; Eskelinen et al., 2012; Kaarlejärvi et al., 2017; Soudzilovskaia et al., 2013). These are often traits related to size (e.g. height) or resource-use strategy, for example, slow–fast traits such as foliar C:N and SLA (Reich, 2014; Westoby et al., 2002; Wright

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et al., 2004). In addition, plant species can respond to environmental changes via intraspecific trait plasticity, that is, within-species trait changes (Liancourt et al., 2015; Moran et al., 2016; Nicotra et al., 2010; Siefert et al., 2015), which can be equal or greater than interspecific variation (Des Roches et al., 2018). Intraspecific trait plasticity can allow communities to respond rapidly to global changes without turnover of species (Jung et al., 2014) or magnify community-level trait change over time (Bjorkman et al., 2018). Therefore, intraspecific traits need to be considered if we are to make accurate predictions about community responses to global changes.

Human-induced alterations in land use and introductions and extirpations of grazers and/or their predators can have huge consequences for the composition, diversity and trait distribution of plant communities (Bakker & Svenning, 2018; Estes et al., 2011; Kaarlejärvi et al., 2017; Post et al., 2019). Herbivores can change community trait composition by targeting and consuming species with tall stature, high SLA and low foliar C:N (Diaz et al., 2007; Evju et al., 2009). Recent studies imply that grazing by mammalian herbivores can also markedly affect intraspecific traits (Firn, Nguyen, et al., 2019; Firn et al., 2017).

Anthropogenic nutrient enrichment, either via airborne deposition or climate warming inducing the release of nutrients from soil organic matter, is a major cause of biodiversity loss and shifts in plant community composition worldwide (Boutin et al., 2017; Stevens, 2019; Tilman et al., 2001). In experimental studies, nutrient addition has also been shown to modify intraspecific traits, for example, to enhance plant height, SLA, foliar N content and leaf greenness (Mudrák et al., 2019; Tatarko & Knops, 2018). These are traits related to rapid growth in resource-rich conditions (Reich, 2014; Wright et al., 2004) and they are therefore likely to confer greater performance and competitive ability under nutrient-rich conditions (Carmona et al., 2019; Suding et al., 2005). Similar intraspecific trait expressions occur in height and SLA (but not foliar C:N or leaf greenness) in response to warming (Bjorkman et al., 2018; Hudson et al., 2011). Moreover, accelerated nutrient turnover in warmer temperatures (Aerts, 2006) should increase above-ground biomass and in turn promote taller plants with a greater competitive ability for light (Elmendorf et al., 2012).

However, not much is known about how mammalian herbivory, increased nutrients and warming interact to affect intraspecific traits, although in nature they occur simultaneously and can either magnify or mitigate each other's impacts on plant communities (Eskelinen et al., 2017; Gough et al., 2007; Kaarlejärvi et al., 2017; Olsen et al., 2014). For example, the absence of grazers can lead to increased biomass and decreased light availability under the canopy (Borer, Seabloom, et al., 2014; Olofsson et al., 2009), and even more so under conditions that are warmer and nutrient-enriched (Kaarlejärvi et al., 2017; Post & Pedersen, 2008), which favour species with traits that are advantageous in light-limited conditions (e.g. tall stems and high SLA; Kaarlejärvi et al., 2017). However, in the presence of grazers, plants experience increased grazing risk, which should promote species and plant individuals with traits associated

with low visibility to, and palatability for, herbivores (e.g. short stems, small SLA, high foliar C:N; Evju et al., 2009).

Intraspecific trait change (i.e. plasticity) in response to contemporary global changes will probably affect population performance (Des Roches et al., 2018; Liancourt et al., 2015) as plants that are able to respond to altered resource availability could also be better competitors under novel conditions (Ashton et al., 2010; Bret-Harte et al., 2001). In consequence, plasticity in traits related to rapid resource-use under warmer and more nutrient-rich conditions could increase competitive ability and population fitness (Firn et al., 2012; Liancourt et al., 2015; but see Siefert & Ritchie, 2016). However, those same trait responses to nutrient enrichment and warming could increase palatability and grazing risk (Evju et al., 2009), translating into decreased abundance and population fitness in grazed conditions (Firn et al., 2012). Whether intraspecific trait change under nutrient-enriched and warmer conditions is manifested in greater species' success may therefore critically depend on grazing.

We experimentally investigated intraspecific trait responses of eight common tundra plant species to mammalian herbivory, fertilization and climate warming. We measured four commonly used traits (vegetative height, SLA, foliar C:N and leaf greenness) linked to resource uptake strategies and competitive ability for light (Evans & Poorter, 2001; Reich, 2014; Wright et al., 2004). We further examined how trait responsiveness to the treatments was linked to species' performance in relation to other species in a community (i.e. its competitive advantage; Goldberg, 1996), measured as change in relative abundance (i.e. the proportion of total community biomass belonging to each species). Our relative abundance measure was based on biomass estimates obtained using the point intercept method (Jonasson, 1988); hereafter called 'abundance' for simplicity. We predicted: (a) Herbivory would decrease intraspecific height and SLA (but not leaf greenness), and increase foliar C:N. (b) Fertilization and warming would increase intraspecific height, SLA and leaf greenness and decrease foliar C:N. (c) These shifts, induced by warming and fertilization, would be more pronounced in the absence of herbivores and smaller in the presence of herbivores. (d) Intraspecific trait change in response to fertilization and warming measured at the individual level would correlate with increased abundance at the community level in the absence of herbivores, but with smaller or decreased abundance in the presence of herbivores.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

This experiment was carried out in NW Finnish Lapland, in Kilpisjärvi (69.055°N, 20.887°E). The experimental site was located on the south-western slope of Mt. Iso-Jehkats 750 m above sea level (Kaarlejärvi et al., 2013). The study site is characterized as species-rich tundra meadow dominated by grasses and forbs (Eskelinen et al., 2017; Kaarlejärvi et al., 2013, 2017). The area is seasonally (June–August) grazed by semidomesticated reindeer

(*Rangifer tarandus tarandus*) of fluctuating herd sizes (Eskelinen & Oksanen, 2006; Heikkinen et al., 2005); recent observations report 9–17 reindeer per km² (Kaarlejärvi et al., 2017). Other important mammalian herbivores, which can markedly affect vegetation, are Norwegian lemmings (*Lemmus lemmus* L.) and grey-sided voles (*Myodes rufocanus* Sund.; Moen, 1990; Virtanen et al., 1997). The mean annual air temperature in the area is –2.0°C (Kaarlejärvi et al., 2017).

We established the experiment in 2009, with a full factorial combination of passive warming, mammalian herbivore exclusion and fertilization, resulting in seven different treatment combinations plus the control. Each treatment combination and control were replicated seven times resulting in a total of 56 experimental plots of 0.8 × 0.7 m (Eskelinen et al., 2017; Kaarlejärvi et al., 2013, 2017). We implemented warming by using hexagonal open top chambers (OTC), a widely used method to investigate effects of warming in tundra areas (Henry & Molau, 1997; Marion et al., 1997). The OTCs were 146 cm wide at the bottom. In this experiment OTCs were used for spring and autumn warming (May–June and August–October). We removed the OTCs for July, the time when the reindeer are present in the area. This allowed equal grazing in all unfenced plots, including the joint treatment of warming and grazing, as OTCs can be a potential grazing barrier for larger herbivores (Moise & Henry, 2010). The other major herbivores, voles and lemmings, could enter the OTCs year around. Our warming treatment therefore extends the growing season at both ends, that is, in April–June and August–September, which matches with predictions for this region (Kivinen et al., 2012). OTCs increased air temperature in June by 1.92°C and in August by 1.23°C compared to the control (Kaarlejärvi et al., 2013). We implemented the herbivore exclusion treatment by establishing circular fences (160 cm in diameter, 100 cm in height, mesh size 10 × 10 mm) embedded 15 cm deep into the soil around each fenced plot (Kaarlejärvi et al., 2013). Additionally, we fenced the entire experimental area with a temporary reindeer fence from the beginning of August to the end of June in the following year. This was done to protect the experiment from straying reindeer outside the normal grazing season, and ensured that grazing pressure was similar in all plots (Kaarlejärvi et al., 2013). We fertilized manually with fast-dissolving NPK fertilizer mixed with 1 L of water to every fertilized plot twice per growing season (mid-June and end of July), resulting in an addition of 9.6 g N, 5.4 g P and 13.2 g K per m² annually. We watered plots not receiving the fertilization treatment with the same amount of water. Mammalian herbivory and ongoing climate warming may accelerate nutrient cycling and increase plant available nutrients (Aerts, 2006; Barthelemy et al., 2018), though to a lesser extent than the fertilization treatment applied in this experiment (Barthelemy et al., 2015; Rustad et al., 2001). The fertilization treatment tested the general role of nutrient limitation for plant growth, following levels used in other experiments in a variety of ecosystems (Borer, Harpole, et al., 2014; Eskelinen et al., 2012; Sitters et al., 2019; Sundqvist et al., 2014). Our treatment also mimicked between-habitat variation in soil

nutrient concentrations in tundra (Eskelinen et al., 2009) and nutrient enrichment effects in some heavily impacted regions (e.g. heavily impacted alpine tundra; Dentener et al., 2006; Galloway et al., 2004).

2.2 | Trait sampling

To investigate intraspecific trait manifestation, we chose eight abundant species in the area and experimental plots based on earlier surveys: *Anthoxanthum odoratum* L., *Bistorta vivipara* (L.) Delarbre, *Ranunculus acris* L., *Sibbaldia procumbens* L., *Solidago virgaurea* L., *Thalictrum alpinum* L., *Vaccinium vitis-idaea* L. and *Viola biflora* L. We selected species encompassing a broad range of sizes (heights) and traits related to rapid resource acquisition (SLA, foliar C:N). We collected the trait data from the eight chosen species from the experimental plots at the end of July to mid-August, in 2018, following a standard sampling protocol (Cornelissen et al., 2003; Perez-Harguindeguy et al., 2013). We collected data on vegetative height (cm) as an indicator for competitive ability under different light conditions (Evans & Poorter, 2001; Westoby et al., 2002). We also collected information on leaf greenness as a surrogate for leaf chlorophyll content which can change in relation to light conditions (Valladares & Niinemets, 2008). Furthermore, we collected data on SLA (mm² per mg dry mass) and foliar C:N; traits associated with slow/fast resource uptake strategy and palatability for herbivores (Diaz et al., 2001, 2004; Evju et al., 2009). Plant height and leaf greenness were measured directly in the field on three vital, fully developed and undamaged individuals per species and plot. The sampled individuals had not been damaged by grazers in the year of sampling (i.e. height in the grazed plots was not a result of plant tissue loss at the time of sampling). This resulted in three replicates per plot. Leaf greenness was measured with a SPAD-502 Plus Chlorophyll Meter (Konica Minolta, Japan). *Thalictrum alpinum* was excluded from leaf greenness measurements, because its leaves were too small for the cuvette of the chlorophyll meter. We sampled leaves for SLA and foliar CN measurements from the same individuals for which we measured height and leaf greenness. In addition, we collected seven more leaves, each from a different individual, for foliar C:N analysis in order to have sufficient plant material. All leaves originating from one plot were pooled. This resulted in one replicate per plot for foliar C:N.

2.3 | Abundance measurements

We used a modified point-intercept method (Jonasson, 1988) with 108 systematically distributed points in 25 × 50 cm² quadrats for measuring species abundance (Kaarlejärvi et al., 2013). In this method, a pin is lowered from each point to the ground and all hits with vegetation are recorded. The number of hits correlates well with biomass (Jonasson, 1988). We used relative species abundance (i.e. the proportion of total community biomass

belonging to each species) as an indicator of species competitive performance in a community. In other studies, biomass has been used as a measure of individual species performance (Liancourt et al., 2015).

2.4 | Data analysis

To assess the interactive effects of herbivore exclusion, fertilization and warming on intraspecific plant height, SLA, foliar C:N and leaf greenness (predictions a, b, c), we applied linear mixed effect models with treatments and species as fixed factors for each measured trait separately. Traits were analysed separately because they were correlated. Plot was used as a random factor to account for the nested sampling design (i.e. that species were collected from the same plots). As treatment effects strongly varied between species, we also ran separate models for each species. For *S. procumbens*, the three-way enclosure \times fertilization \times warming interaction was omitted from the models as it was absent from this treatment combination. We assessed the significance of the treatment effects using *F* tests. We used model diagnostic plots to check the homogeneity of variances and the normality of errors (Crawley, 2007) and the data were log- or square-root transformed whenever necessary (see Table 1; Table S1 for more information of transformed variables).

Furthermore, we calculated trait change according to Equation (1):

$$\text{Trait change}_{i,j,k} = \text{mean}(\text{trait value}_{i,j,k}) - \text{mean}(\text{trait value}_{i,j=C,k}), \quad (1)$$

where *i* refers to one of the eight species, *j* is one of the seven different treatments and *k* is one of the four measured traits. *C* refers to all control plots.

For the species abundance data, we calculated change in the same manner (Equation 2) based on abundance data collected in 2018.

$$\text{Change of relative abundance}_{i,j} = \text{mean}(\text{relative abundance}_{i,j}) - \text{mean}(\text{relative abundance}_{i,j=C}), \quad (2)$$

where *i* refers to one of the eight species and *j* is one of the seven different treatments, *C* refers to all control plots.

To assess whether a change in intraspecific trait values (i.e. plasticity) was linked to a change in relative abundance and to assess how this relationship depended on herbivory (prediction d), we fitted linear mixed effects models with change in relative abundance as the response variable and herbivore exclusion, trait value change and their interaction as fixed explanatory factors. We ran separate models for each measured trait, but not for each species because there were too few data points (i.e. one replicate per species and treatment combination); however, we added species as a random effect.

We used the 'lme4' package (Bates et al., 2015) to run linear mixed effect models, the 'car' package for assessing the significance of the treatments effects (Fox & Weisberg, 2019), the 'dplyr' package for data manipulation (Wickham et al., 2018) and the 'ggplot2' package for plotting (Wickham, 2016) in R statistical software (version 3.6.1; R Core Team, 2019).

TABLE 1 Results of mixed effects models testing the effects of enclosure, fertilization, warming and their interactions on intraspecific trait values of height, SLA, foliar C:N and leaf greenness across eight studied species

Source of variation	Height ^a		SLA ^a		Foliar C:N ^b		Leaf greenness	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Enclosure	111.9	<.001	36.8	<.001	41.5	<.001	0.7	.399
Fertilization	31.1	<.001	5.8	.02	20.5	<.001	19.2	<.001
Warming	16.6	<.001	3.3	.08	40.4	<.001	0.3	.565
Species	519.6	<.001	474.3	<.001	1,359.2	<.001	208.3	<.001
E \times F	<0.1	.806	3.9	.053	3.6	.063	0.2	.628
E \times W	3.0	.09	<0.1	.814	4.9	.032	0.7	.398
E \times S	4.9	<.001	3.1	.003	12.5	<.001	3.8	<.001
F \times W	0.3	.577	0.3	.958	2.8	.103	2.4	.128
F \times S	8.6	<.001	2.3	.026	4.1	<.001	3.1	.005
W \times S	7.8	<.001	11.7	<.001	29.2	<.001	18.2	<.001
E \times F \times W	0.8	.385	0.2	.678	<0.1	.89	<0.1	.826
E \times F \times S	9.9	<.001	6.9	<.001	2.5	.016	0.9	.487
E \times W \times S	2.7	.009	0.8	.562	4.0	<.001	0.8	.533
F \times W \times S	2.6	.013	1.2	.31	5.7	<.001	0.7	.679
E \times F \times W \times S	1.0	.441	2.5	.019	4.9	<.001	1.3	.261

Note: Significant results ($p < .05$) are in bold and marginally significant results ($p < .1$) are in italics. Abbreviations: E, enclosure; F, fertilization; S, species; SLA, specific leaf area; W, warming.

^aLog-transformed.

^bSquare-root transformed.

3 | RESULTS

3.1 | Interactive effects of herbivore exclusion, fertilization and warming on plant intraspecific trait responses

Herbivore exclusion, fertilization and warming all exhibited significant positive main effects on height across all species (Figure 1a; Table 1). Plants were, on average, 50% taller inside fences than in grazed plots, while fertilization increased height by 28% and warming increased height by 11%. These general patterns were also valid at the species level (Figure S2; Table S1). Herbivore exclusion interacted with fertilization and this interaction also depended on species (Table 1, three-way $E \times F \times S$ interaction). Overall, across the species, fertilization tended to have greater positive impact when herbivores were excluded (Figure 1a, but there was no significant two-way interaction); at the individual species level this was the case especially with some

tall-statured species (e.g. *S. virgaurea*), while with some smaller species (*V. biflora*) the positive impact of fertilization was greater when herbivores were present (Figure S2e,h). Across the species, the effect of herbivore exclusion on height significantly interacted with warming such that when grazers were present, warming increased height compared to ambient conditions; however, when grazers were absent warmed and ambient plots did not differ from each other ($E \times W$ interaction, Figure 1a; Figure S1; Table 1). However, herbivore exclusion was still the strongest overall predictor of height (Figure 1a).

Across all species, herbivore exclusion increased SLA by 19% and fertilization by 10%, while warming had no effect on SLA (Figure 1b; Table 1). The positive effect of fertilization on SLA was stronger inside fences than in grazed plots ($E \times F$ interaction, Figure 1b; Figure S3; Table 1; Table S1).

Herbivore exclusion reduced foliar C:N by 11% and fertilization reduced it by 7.5%. Warming, however, increased foliar C:N by 12% across all species (Figure 1c; Table 1). The same pattern was valid at

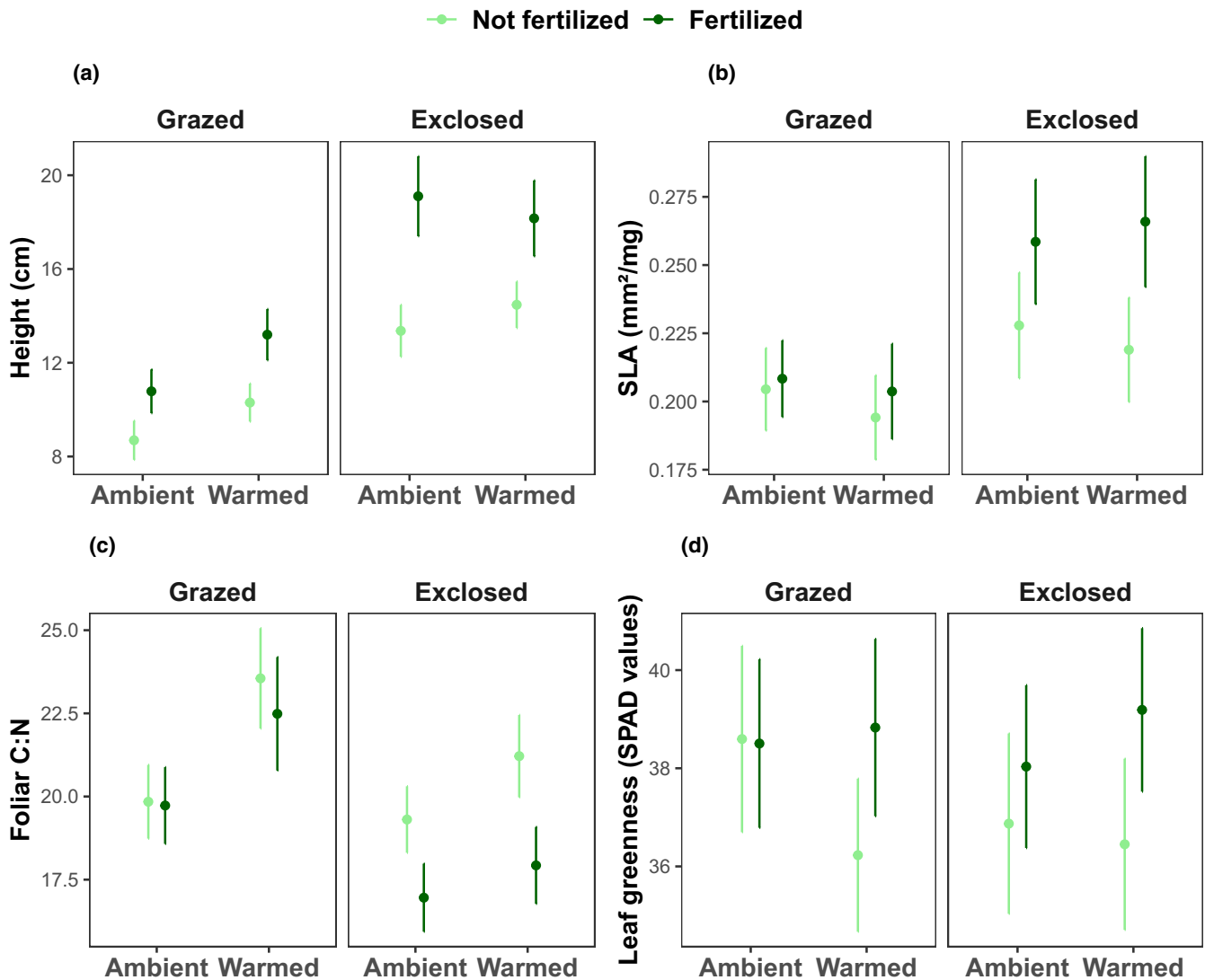
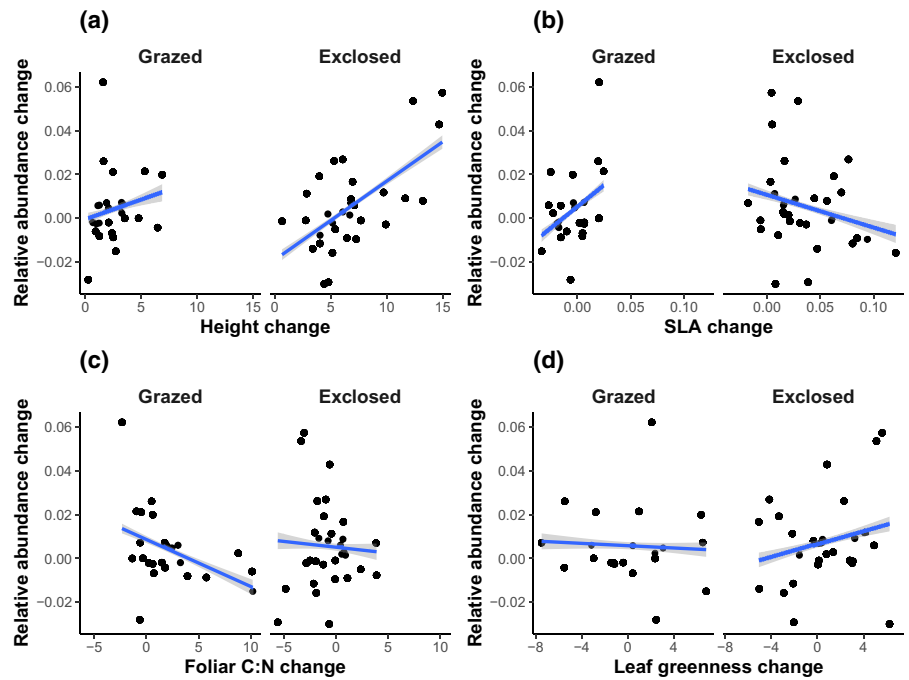


FIGURE 1 Trait values (mean \pm SE) of (a) height, (b) specific leaf area (SLA), (c) foliar C:N and (d) leaf greenness (SPAD) across eight tundra species in all treatment combinations of enclosure, fertilization and warming ($n = 56$). Leaf greenness values were measured for three individuals per plot with the exception of *Thalictrum alpinum*, where the leaves were too small for the chlorophyll meter cuvette

FIGURE 2 Relationship between relative abundance change and changes in (a) height, (b) specific leaf area (SLA), (c) foliar C:N or (d) leaf greenness. The fitted line is a linear regression. Each data point represents the mean per species and treatment combination, resulting in eight (species) times seven (treatment combinations) points. Based on the calculations in Equations (1) and (2), there are fewer data points in the grazed panels because grazed only plots were used as controls



the species level (Figure S4). Herbivory also tended to mediate the effect of fertilization on foliar C:N such that fertilization reduced C:N more inside fences than outside fences (marginally significant $E \times F$ interaction, Figure S4; Table S1). In addition, warming increased foliar C:N more strongly in grazed than in fenced plots ($E \times W$ interaction, Figure 1c; Figure S4; Table 1; Table S1).

Fertilization increased leaf greenness, but neither warming nor grazing showed any effects on greenness across the species (Figure 1d; Table 1). Leaf greenness of individual species showed mixed responses to herbivore exclusion, fertilization and warming (Figure S5; Table S1).

3.2 | Intraspecific trait changes and change in relative abundance

We found evidence that trait changes were associated with changes in relative abundance. The direction of this relationship (positive or negative) depended on the trait and on herbivory (Figure 2a–d). Height change (i.e. height plasticity) was associated with increases in relative abundance, indicating that height plasticity in response to warming and fertilization translates to abundance gain. However, herbivores modified this relationship so that height plasticity increased relative abundance more strongly under fenced than under grazed conditions (trait change \times E interaction, Figure 2a; Table 2). For SLA we observed the opposite; SLA change in response to warming and fertilizing was related to decreased relative abundance under fenced conditions, and increased relative abundance under grazed conditions (trait change \times E interaction, Figure 2b; Table 2). In other words, plants that were more plastic with respect to SLA increased their relative abundance only when grazers were present. Herbivores did not affect the relationship between either foliar C:N or leaf greenness and relative abundance. However, plasticity in greenness was associated with an increase in relative abundance (Table 2).

TABLE 2 Results of four mixed effects models testing the effect of trait change (height, SLA, foliar C:N and leaf greenness) and its interaction with grazing on relative abundance change across species. In the models, species was treated as a random effect

Source of variation	Relative abundance change		R^2 marginal	R^2 conditional
	<i>F</i>	<i>p</i>		
Height change	334.47	<.001	.17	.48
Exclosure (E)	103.97	<.001		
<i>E</i> \times Height change	36.54	<.001		
SLA change	89.20	<.001	.06	.54
Exclosure (E)	74.49	<.001		
<i>E</i> \times SLA change	46.42	<.001		
Foliar C:N change	3.18	.074	.007	.50
Exclosure (E)	13.82	<.001		
<i>E</i> \times Foliar C:N change	3.41	.065		
Leaf greenness change	18.93	<.001	.02	.48
Exclosure (E)	9.97	.002		
<i>E</i> \times Leaf greenness change	<0.1	.785		

Note: Significant results ($p < .05$) are in bold and marginally significant results ($p < .1$) are in italics.

4 | DISCUSSION

Recent studies suggest that climate warming and nutrient enrichment can lead to pronounced intraspecific trait shifts (Bjorkman et al., 2018; Firn, McGree, et al., 2019) and highlight the need to assess trait responses to multiple global changes that mimic future novel conditions (Donelson et al., 2018; Matesanz et al., 2010). We

found that while increased temperature and nutrients modified intraspecific traits, grazing was a key factor affecting intraspecific trait change in a tundra plant community. Importantly, we also demonstrate that these trait responses to environmental changes can link to abundance changes at the community level; however, these relationships are contingent on mammalian herbivory.

Our finding that fertilization and, to a lesser extent warming, increased intraspecific height and SLA and reduced foliar C:N supports our prediction and is consistent with earlier studies about the effects of warming and fertilization separately (Baruah et al., 2017; Bjorkman et al., 2018; Henn et al., 2018; Hudson et al., 2011; Siefert & Ritchie, 2016) or in combination (Campioli et al., 2012). These findings emphasize the fact that species are able to exhibit plasticity in their responses to higher nutrient levels and warmer temperatures: becoming taller, and altering traits related to resource use (SLA, foliar C:N). These traits can improve species competitive ability in resource-rich and light-limited conditions (Suding et al., 2005) and consequently influence species' coexistence (Callaway et al., 2003; Turcotte & Levine, 2016). Importantly, plasticity in these traits can make species less vulnerable to climate warming and nutrient eutrophication as plasticity can allow species to cope with novel conditions (Nicotra et al., 2010).

However, we also found that grazing had a stronger effect on intraspecific traits than either warming or fertilization. Our finding that, in the absence of grazers, plants greatly increased height and SLA and reduced foliar C:N supports our prediction and is in line with results from previous studies (Firn, Nguyen, et al., 2019; Whitworth-Hulse et al., 2016). When grazed repeatedly, plant individuals should invest less resources in stems and leaves (Milchunas et al., 1988), reducing visibility and palatability to grazers, and favouring shorter stature and smaller SLA (Diaz et al., 2007). Avoiding grazing is likely to come at the expense of optimizing resource uptake, while in ungrazed, highly competitive conditions optimization of resource uptake (e.g. light) is essential (Diaz et al., 2001).

In addition, fertilization increased SLA and for some species also had a positive impact on height, and reduced foliar C:N more in the absence of grazers. This corroborates our prediction and highlights that herbivores need to be accounted for when assessing the effect of nutrients on intraspecific traits. These results somewhat contradict findings by Firn et al. (2012) and Firn, McGree, et al. (2019) that the effect of herbivores on leaf traits either did not interact with fertilization or that the impact of fertilization was greater when herbivores were present. The long grazing history (Heikkinen et al., 2005) and relatively intense grazing at our site (Kaarlejärvi et al., 2017) may explain these disparate results. Earlier studies from the same system have shown that the presence of grazers mitigates the positive fertilization effect on lowland species' invasion and performance (Eskelinen et al., 2017; Kaarlejärvi et al., 2013) and reduces the loss likelihood of short-statured, low SLA species (Kaarlejärvi et al., 2017). The results from the present study show that, even under nutrient-rich conditions, herbivory promotes smaller stature and SLA and higher foliar C:N, and these effects extend to within-species variation.

Earlier studies have shown that tall-statured species are more likely to benefit from nutrient addition and warming, emphasizing

the importance of interspecific trait differences driving shifts in competitive dominance under global changes (Bjorkman et al., 2018; DeMarco et al., 2014; Eskelinen & Harrison, 2015; Kaarlejärvi et al., 2017; Klanderud, 2008). We found that plants exhibiting greater height increase in response to nutrient addition and warming also showed greater abundance increases, suggesting that height plasticity contributes to community trait change. Not only between-species differences, but also within-species trait variability can drive community and ecosystem responses to global changes (Liancourt et al., 2015; Nicotra et al., 2010).

Furthermore, we found that the relationship between trait change in height and SLA and relative abundance change was contingent on herbivory. Greater height plasticity was more beneficial for relative abundance in the absence of herbivores, as we predicted. In contrast to our prediction we found the opposite for SLA, as higher SLA plasticity lead to an increase in relative abundance in the presence of herbivores. Greater height plasticity in ungrazed plots is probably linked to better competitive ability for light in high-biomass and light-limited conditions, promoting greater abundance in a community (Turcotte & Levine, 2016). However, higher SLA plasticity in the presence of herbivores might rather be linked to plants' capacity to compensate for grazing damage (Brathen & Odasz-Albrigtsen, 2000). The combination of fertilization and warming, that is, resource-rich and otherwise favourable conditions for growth, can favour traits that support compensatory growth (e.g. high SLA, low foliar C:N; Augustine & McNaughton, 1998; Coley et al., 1985). This aligns with the overcompensation theory (McNaughton, 1983), stating that grazing can stimulate plant growth and enhance persistence especially under nutrient-rich and warmer conditions (Coley et al., 1985; Ramula et al., 2019). Overall, our results highlight that herbivory is a major factor influencing how much intraspecific trait plasticity facilitates performance and needs to be taken into account when assessing plant traits under warmer and more nutrient-rich conditions.

Overall, we observed strong general patterns despite the variation caused by species-specific differences. However, individual species still differed in their responses. For example, *V. biflora*, a small-statured species, increased height under nutrient-rich conditions more in grazed than in fenced conditions, whereas *S. virgaurea*, a tall-statured species, grew taller in nutrient-rich and fenced conditions. It is possible that repeated biomass loss to herbivores reduces any long-term benefit from nutrients especially in inherently tall species, possibly because of smaller root: shoot ratio in high nutrient availability and consequently less tolerance to repeated herbivory (Olff et al., 1990; Strauss & Agrawal, 1999). In contrast, inherently small-statured species, that can avoid being grazed may benefit from nutrients and competition-free environment in grazed systems. Our results, therefore, emphasize that intraspecific trait plasticity is also controlled by different factors for different species (Albert et al., 2010; Lang et al., 2020; Liancourt et al., 2015) and more research is needed to disentangle which inherent properties of species dictate these responses.

To conclude, our findings highlight the importance of intraspecific trait plasticity as a mechanism to cope with climate warming,

nutrient enrichment and changing grazing regimes. Our results also highlight the need to consider interdependencies among these global change drivers when assessing intraspecific trait change. While earlier studies have identified mammalian herbivory as a key factor modulating the impacts of nutrient enrichment and climate warming on plant community composition, productivity and diversity (Borer, Seabloom, et al., 2014; Kaarlejärvi et al., 2017; Post & Pedersen, 2008), we identified mammalian herbivory as a key factor mediating their impacts on intraspecific traits. Furthermore, herbivory also affected how intraspecific trait plasticity translates to changes in relative abundance in a community. These results suggest that decisions on management and regulation of grazer and predator populations play critical roles in altering trait change in tundra and its consequences on ecosystem functioning in the Anthropocene (Bakker & Svenning, 2018; Estes et al., 2011; Lundgren et al., 2020).

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at <https://doi.org/10.6084/m9.figshare.13019738.v1>.

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SUPPORTING INFORMATION

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

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