Experimental warming alters migratory caribou forage quality

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Abstract. Global declines in caribou and reindeer (*Rangifer*) populations have drawn attention to the myriad of stressors that these Arctic and boreal forest herbivores currently face. Arctic warming has resulted in increased tundra shrub growth and therefore *Rangifer* forage quantity. However, its effects on forage quality have not yet been addressed although they may be critical to *Rangifer* body condition and fecundity. We investigated the impact of 8 yrs of summer warming on the quality of forage available to the Bathurst caribou herd using experimental greenhouses (*n* = 5) located in mesic birch hummock tundra in the central Canadian Low Arctic. Leaf forage quality and digestibility characteristics associated with nutrients (nitrogen and phosphorus), phenolics, and fiber were measured on the deciduous shrub *Betula glandulosa* (an important *Rangifer* diet component) at six time points through the growing season, and on five other very common vascular plant and lichen species in late summer. Experimental warming reduced *B. glandulosa* leaf nitrogen concentrations by ~10% in both late June and mid-July, but not afterwards. It also reduced late summer forage quality of the graminoid *Eriophorum vaginatum* by increasing phenolic concentrations 38%. Warming had mixed effects on forage quality of the lichen *Cetraria cucullata* in that it increased nutrient concentrations and tended to decrease fiber contents, but it also increased phenolics. Altogether, these warming-induced changes in forage quality over the growing season, and response differences among species, highlight the importance of *Rangifer* adaptability in diet selection. Furthermore, the early season reduction in *B. glandulosa* nitrogen content is a particular concern given the importance of this time for calf growth. Overall, our demonstration of the potential for significant warming impacts on forage quality at critical times for these animals underscores the importance of effective *Rangifer* range conservation to ensure sufficient appropriate habitat to support adaptability in forage selection in a rapidly changing environment.

Key words: climate change; fiber; greenhouse; lichen; nutrients; nutrition; phenolics; Rangifer; shrub; tundra.

Introduction

Global declines in caribou and reindeer herds across the Arctic suggest that landscape changes due to resource development and climate warming, as well as increases in hunting, insect harassment, disease, and predation, may be detrimental for this dominant Arctic herbivore (Vors and Boyce 2009, Festa-Bianchet et al. 2011, Witter et al. 2012, Fauchald et al. 2017). Caribou and reindeer (hereafter called *Rangifer*) population size dynamics have been subject to strong natural environmental variation in the past (Jefferies et al. 1992, Morneau and Payette 2000, Zalatan et al. 2006). However, the extent to which their populations are also being affected by recent anthropogenic impacts remains unclear. Among all the potential stressors to *Rangifer* populations, climate change impacts may be the most complex and most uncertain (Weladji et al. 2002, Sharma et al. 2009, Fauchald et al. 2017).

There is extensive evidence that Arctic vegetation is changing in ways that may alter both *Rangifer* forage

quantity and quality (Post and Forchhammer 2008, Elmendorf et al. 2012b). For example, deciduous shrubs are heavily browsed by *Rangifer* in summer (Boertje 1984, Manseau et al. 1996). Therefore, the well-documented recent trend of increased shrub growth across the Arctic (Tape et al. 2006, Epstein et al. 2012, Ju and Masek 2016) generally translates to increased summer forage quantity. By contrast, the impacts of climate warming on forage quality remain largely unknown (Turunen et al. 2009, Fauchald et al. 2017), and may be highly relevant to the body condition and fecundity of wild *Rangifer* (Crête and Huot 1993, Couturier et al. 2009). During the growing season, *Rangifer* select forage based on forage abundance and nutrient content (Mårell et al. 2006, Skarin et al. 2008) and digestibility (White and Trudell 1980, Côté 1998). Preferred forage has relatively high digestibility and high protein content (White and Trudell 1980, Côté 1998). It is critically important to *Rangifer* population condition because maximizing nutritional gain during the growing season is necessary for calf survival, fecundity, and fat and protein accretion before winter (Crête and Huot 1993, Couturier et al. 2009).

Forage is of highest nutritional value when it has high nutrient content, particularly nitrogen (N) and

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phosphorus (P), low fiber and lignin, and low phenolic concentrations (Van Soest 1994). Nitrogen is essential for protein accretion, with highest demands in the early to mid-summer period to support lactation (Crête and Huot 1993, Taillon et al. 2013). Phosphorus is also critical at that time to support bone development and antler regrowth (Moen and Pastor 1998). Concurrently, vascular plant leaf nitrogen and phosphorus concentrations are also at their seasonal peak in early summer (Chapin et al. 1980, Johnstone et al. 2002). Meanwhile, concentrations of phenolics, fiber, and lignin are inversely related to forage quality (Van Soest 1994). Phenolics reduce protein absorption by binding with dietary proteins and digestive enzymes (Appel 1993). High fiber and lignin contents increase digestion time since their complex chemical structures require more extensive processing by rumen bacteria (Buxton and Redfearn 1997). Although increased time spent feeding may partially compensate for decreased diet quality (Hamel and Côté 2009), rates of digestion and excretion impose a limit on the amount that can be consumed (Perez-Barberia and Gordon 1998).

Climate warming may impact all of the above-mentioned chemical properties associated with *Rangifer* forage quality. For example, increased air temperatures in experimental greenhouses or open-topped chambers tend to decrease N and/or P concentrations in deciduous and graminoid vascular plants (Dormann and Woodin 2002, Kaarlejarvi et al. 2012, Doiron et al. 2014), although this effect is not observed at all sites (Welker et al. 2005, Zamin 2013). These reduced nutrient concentrations may be due to growth dilution, whereby the additional new biomass associated with warming dilutes accumulated N and P (Shaver and Chapin 1980). Meanwhile, experimental warming has had mixed impacts on phenolic concentrations, with variation in responses associated with species, leaf age, site characteristics, and timing of sampling (Graglia et al. 2001, Hansen et al. 2006, Nybakken et al. 2011, Kaarlejarvi et al. 2012). Although warming impacts on fiber or lignin in Arctic plants have not yet been investigated, studies in other systems indicate the effects may be highly species-specific (Lenart et al. 2002) or chemically specific (e.g., lignin vs. cellulose; Chen et al. 2008). For example, warming may increase fiber concentrations if it causes species to increase leaf size and therefore structural investment within those larger leaves (Milla and Reich 2007), or if it causes increases in leaf mass per unit area (i.e., decreases specific leaf area; Hudson et al. 2011). Altogether, this summary of previous research indicates high variability in forage quality chemical responses to warming among individual plant species at particular sites across the Arctic (Dormann and Woodin 2002, Welker et al. 2004, Kaarlejarvi et al. 2012).

Climate change may also alter *Rangifer* forage quality via impacts on leaf nutrient phenology. Leaf nutrient concentrations tend to be highest at emergence and decrease through the growing season, particularly for deciduous shrubs and forbs (Chapin et al. 1980, Johnstone et al. 2002). The earlier onset of the growing season in the Arctic has led to earlier leaf emergence (Post and Forchhammer 2008). Since spring climate strongly influences peak nitrogen concentrations (Doiron et al. 2015), phenological patterns of leaf nutrient forage quality are being affected. For example, analyses of multi-decadal records indicate that warm, early snowmelt years can significantly advance spring nitrogen concentration peaks in Arctic graminoids, resulting in a trophic mismatch with their geese herbivores (Doiron et al. 2015). In contrast to nutrients, phenolic concentrations tend to be low in the spring and increase later in the growing season (Chapin et al. 1986, Hansen et al. 2006) as leaf cell development shifts from early rapid growth toward structural differentiation and defense (Herms and Mattson 1992). Altogether, these physiological changes associated with leaf phenology imply that the impacts of warming on differing components of forage quality may be variable across the growing season.

Here, we report a comprehensive study of experimental warming impacts on multiple properties of forage quality in several of the major plant and lichen species within the Bathurst caribou herd's summer range. The Bathurst caribou herd is part of the subspecies *Rangifer tarandus groenlandicus* L. that extends across all of the Canadian Low Arctic (Festa-Bianchet et al. 2011). Specifically, we investigated impacts on nitrogen, phosphorus, fiber, lignin, and phenolic concentrations in the following six plant species: the deciduous shrub *Betula glandulosa* (Michx.), graminoid *Eriophorum vaginatum* (L.), evergreen shrubs *Rhododendron subarcticum* (Harmaja [formerly *Ledum decumbens* (Aiton) Lodd. ex Steud.]) and *Vaccinium vitis-idaea* (L.), and lichens *Cetraria cucullata* (Bellardi) Kärnefelt & Thell and *Cladina rangiferina* (L.) Nyl. These six species were chosen based on their prevalence in the diets of North American migratory tundra *Rangifer* and/or abundance in typical mesic Low Arctic vegetation (CAVM 2003). Deciduous shrubs constitute about 45% of summer diets of *Rangifer* in North America (see review of dietary composition studies in Appendix S1: Tables S1 and S2), with *B. glandulosa* heavily browsed at least in the eastern Arctic (Manseau et al. 1996). Furthermore, leaf biomass of this species was almost doubled in plots from which *Rangifer* were excluded at our research site in the Canadian central low Arctic (Zamin and Grogan 2013). Graminoids may constitute around 6% of summer diets and around 13% of spring and fall diets (Appendix S1: Table S1), and *E. vaginatum* is known to be among preferred graminoid species (White and Trudell 1980, Boertje 1984). Evergreen shrubs are generally marginal to *Rangifer* diets in North America (Appendix S1: Table S1) but are highly abundant in mesic Low Arctic vegetation (CAVM 2003, Zamin et al. 2014). Furthermore, *Rangifer* exclusion has been shown to enhance evergreen shrub biomass at our Daring Lake study site (Zamin and Grogan 2013). Last, lichens make up 15–55% of diets in the growing season (Appendix S1: Table S1), with the two species assessed in this study among the most abundant in birch hummock tundra (i.e., comprising

58% of lichen biomass; Zamin et al. 2014), and preferentially consumed by *Rangifer* (White and Trudell 1980, Witter 2010; Appendix S1). Altogether, this integrated approach examining a range of forage properties of the most common vascular plant and lichen species in this Low Arctic tundra ecosystem should allow for more reliable predictions of climate warming impacts on *Rangifer* forage quality.

This study builds on previous research from the same site using the same greenhouse infrastructure that had already demonstrated that warming increases biomass for all the major vascular plant species in this vegetation type, and decreases biomass for the lichens (Zamin et al. 2014). Similar results have been observed in a wide range of other analogous tundra studies (Chapin et al. 1995, Elmendorf et al. 2012*a*), leading to the conclusion that warming is likely to enhance the quantity of most *Rangifer* forage plant species, except perhaps lichens (Cornelissen et al. 2001). Here, we focus on experimental warming impacts on *Rangifer* forage quality by comparing tissues of all the above species that were sampled in late summer. In addition, we characterized the temporal pattern of warming impacts on *B. glandulosa* forage quality by sampling leaves multiple times from late spring through to the end of summer. Based on the previously documented plant growth responses to experimental warming at our site (Zamin et al. 2014), and our review above of warming impacts on plant leaf chemical components that are critical to *Rangifer* forage quality, we hypothesized that: (1) enhanced growth due to warming will decrease late summer concentrations of nutrients, as well as phenolics and fiber, and these decreases will be largest in *B. glandulosa* and *E. vaginatum* since they have higher growth rates than the lichens and evergreen shrubs (species comparison); and (2) enhanced growth due to warming will decrease *B. glandulosa* leaf nutrient concentrations in spring and early summer (phenology of birch leaf forage quality).

Materials and Methods

Site and treatment

This study was conducted in mesic birch (*Betula* spp.) hummock tundra vegetation near the Tundra Ecosystem Research Station, Daring Lake, Northwest Territories (64°52′ N, 111°33′ W) in the central Canadian Low Arctic. Diel temperatures range from an annual minimum of −38° ± 0.7°C (mean ± SE) in January to a maximum of 20° ± 0.4°C in July, and mean annual rainfall is about 138 ± 13 mm (B. Reid, *unpublished data*, 1996–2011). Birch hummock tundra is part of the erect dwarf shrub tundra category of Arctic vegetation types (CAVM 2003), where the maximum shrub height is 30 cm, and evergreen shrubs and lichens dominate the vegetation (48% and 25% of aboveground biomass, respectively; Zamin et al. 2014). *B. glandulosa* and *E. vaginatum* are the most abundant deciduous shrub and graminoid, respectively, each

constituting around 7% and 5% respectively, of the aboveground vascular plant biomass (Zamin et al. 2014). *Salix* spp. are rare in mesic birch hummock tundra, but do occur in other vegetation types at the site. This area is part of the summer range of the migratory Bathurst caribou herd. The Bathurst caribou herd increased during the early 1980s and peaked in 1986 at over 450,000 individuals (Adamczewski et al. 2009). Between 1986 and 2012, the herd declined to ~35,000 individuals (Adamczewski et al. 2009), remained stable for a few years, and then further declined to as few as 16,000 individuals in 2015 (GNWT 2016).

Experimental plots were set up in a valley near the Tundra Ecosystem Research Station. Vegetation patches of similar species composition, relative abundances, and topography were identified in a broad gently sloping valley in early July 2004 and randomly assigned to treatment or control (n = 5 each). The experimental warming was achieved with A-frame greenhouses (1.8 × 4.7 m; n = 5) covered with heavy polyethylene film (150 μm) that reduced mean photosynthetically active radiation (PAR) in daytime by 32% (Farnsworth 2007). Previous studies with a 50% light reduction shading treatment in moist low Arctic tundra vegetation indicate that decreased light availability reduces overall ecosystem-level production, but has relatively little impact on community composition and species relative abundances compared to increased temperature (greenhouses) or nutrient availability (fertilization; Chapin et al. 1995). Small vent holes (20 cm tall) in the apex of each end of the greenhouses promote air flow to restrict extreme temperatures and relative humidity levels. The experiment was a summer-only warming treatment, i.e., each summer since 2004, the plastic film was put up in early–mid June and taken down in late August–early September. In the year of this study (2011), the plastic film was installed by 16 June. The greenhouses have been shown to raise mean air and soil temperatures at 2–10 cm depth by 2.1°2.4°C over the summer period, but have no significant effect on soil moisture, even in the top 0–4 cm depth interval (Zamin et al. 2014).

Vegetation sampling

To compare forage quality properties among species, samples were harvested from all individual plants or ramets of each species within a 40 × 40 cm area of each plot on 14–15 August 2011. All leaves from within this 40 × 40 cm area were collected from *B. glandulosa*, *E. vaginatum*, *R. subarcticum*, and *V. vitis-idaea*, as well as all biomass from the lichen species, *C. cucullata* and *C. rangiferina*. All samples were stored in a −20°C freezer until laboratory analyses.

To characterize changes in foliage quality of *B. glandulosa* through the growing season, leaves were collected from each plot every 2 weeks from 28 June (approximately 2 weeks after leaf emergence that year; E. Humphreys, *unpublished data*) to 2 September 2011 (when the leaves had started to change color, but not yet senesced;

Zamin, T.J., *personal observation*). At each sampling date, leaves were collected from throughout the canopy of only one individual plant or ramet, and that individual was then tagged to ensure it was not resampled later in the summer. Leaves were stored in a $-20°C$ freezer until laboratory analysis.

Chemical analyses

All forage quality properties were analyzed for the late summer multispecies comparison and a subset analyzed for the *B. glandulosa* phenological analysis. Specifically, neutral-detergent fiber (NDF), acid-detergent fiber (ADF), acid-detergent lignin (ADL), nitrogen (N), phosphorus (P), and total phenolic concentrations were determined for all samples in the mid-August multi-species comparison. The *B. glandulosa* samples collected every 2 weeks throughout the growing season were analyzed for concentrations of N, P, and total phenolics, but not fiber or lignin contents because of insufficient sample mass.

Prior to chemical analysis, all samples were homogenized via grinding and recombined to the species level in cases where leaves had been further separated to age classes. Samples were oven-dried at 40°C and then ground to a 0.5 mm particle size (IKA MF 10 Microfine grinder, Staufen, Germany). In the evergreens, leaves had been separated into new leaves (current year's growth) and old leaves (all past years' live growth). These samples were recombined for forage analysis because, in most instances, *Rangifer* consumption would include both categories since they are interspersed on the same plant due to dense branching. Specifically, in the case of N, P, and phenolics, the chemical analyses were performed on the two age classes, and then results weighted by the relative proportion of new and old leaves in individuals from that plot. For fiber, the tissue was recombined prior to chemical analysis using the average ratio of new to old leaves for each treatment to determine the appropriate recombined sample.

Samples were prepared and analyzed using standard laboratory techniques for the corresponding chemical analyses. ADF, NDF, and ADL were analyzed using the ANKOM Technology method and an ANKOM Fiber Analyzer (Van Soest 1963, ANKOM Technology 2003*a*, *b*, 2011). Total nitrogen was analyzed via dry combustion on an Elemental Analyzer (Elementar, Hanau, Germany), and total phosphorus using acid digestion (U.S. EPA 2001) and inductively coupled plasma-atomic emission spectrometry (ICP-AES; Varian Vista AX, Palo Alto, California, USA). Total phenolic concentrations were analyzed using the Folin-Ciocalteu assay (Folin and Ciocalteu 1927, Bärlocher and Graça 2005) and a spectrophotometer (SpectraMax Plus[384], Molecular Devices, Sunnyvale, California, USA). The assay used tannic acid as a standard, and therefore all total phenolic concentrations represent tannic acid equivalents. Tannins are the subgroup of phenolics known to precipitate proteins

(Appel 1993), themselves including hydrolysable tannins and condensed tannins. Concentrations of hydrolysable tannins have been shown to strongly positively correlate with total phenolics (Salminen et al. 2004).

Statistical analyses

Principal components analyses were used to analyze the effects of warming on overall forage chemistry for each species. Treatment differences were tested using student's *t* tests on the plot (site) scores from the first principal component (PC1). Only replicates that had data for all six chemical properties could be included in the ordinations, which led to $n = 3$ for the *E. vaginatum* control and the *C. rangiferina* greenhouse treatment. All other species had n of 4–5 per treatment for the ordinations (Appendix S2).

Warming impacts on single forage parameters were assessed with univariate tests for each species. All species–chemical combinations were analyzed separately. A linear model testing for treatment-by-species interactions on a given forage property would have assumed all species responses were independent, which was not biologically meaningful, and multivariate analysis of variance could not be conducted since the assumptions were not met. Therefore, Student's *t* tests or Wilcoxon rank sum tests were conducted, depending on whether the parametric assumptions could be met. Since each species had six tests conducted (i.e., NDF, ADF, ADL, N, P, phenolics), sequential Bonferroni corrections (Holm 1979) were applied to the corresponding *P*-values to adjust for Type I error within species. Lastly, the effects of the warming treatment and sampling date on *B. glandulosa* forage quality properties through the growing season were investigated using a repeated measures ANOVA.

Transformations were applied as appropriate for the data. All proportion data (e.g., ADF, NDF, ADL, N, and P concentrations) were square-root-arcsine transformed prior to analysis. Analyses of phenolic concentrations were conducted on the raw data, with the exception of *B. glandulosa* mid-August leaf samples, for which a log-transformation was used to achieve normality and homoscedasticity of the data prior to the analysis. Last, statistical analysis of PC1 scores was conducted on the original scores for all species except *R. subarcticum* for which the scores were log-transformed prior to analysis.

All data and test results are available in the Appendix material. All sample means, standard errors, and sample sizes are reported in Appendices S2 and S3, and statistical test results are available in Appendices S4–S7. Statistical test results with $P < 0.10$ (post-Bonferroni correction for univariate analyses) are mentioned in the text and delineated in the figures, and results with $P < 0.05$ are discussed. All analyses were conducted in R 3.1.3 (R Core Team 2015) and PCAs conducted using the vegan package (Oksanen et al. 2015).

Results

Forage quality in response to experimental warming in late summer

Our analysis demonstrates that 8 yrs of experimental warming altered the overall chemical composition of the leaves and lichens of several dominant species in birch hummock tundra (Fig. 1; Appendix S5). These effects were strongest on the two lichen species, *C. cucullata* and *C. rangiferina*, in which warming was associated with an increase in nutrients, phenolics, ADF, and ADL (*C. cucullata*) in the ordination, with significant treatment differences in PC1 scores (Fig. 1; *C. cucullata*: $t = 6.7$, $P < 0.01$; *C. rangiferina*: $t = -3.8$, $P < 0.01$). Specifically, warming increased N concentration in *C. cucullata* by 28% (Fig. 2; Appendix S6; $t = -4.1$, $P < 0.01$ [Bonferroni corrected P values presented]), and increased P concentration in *C. cucullata* and *C. rangiferina* by 45% and 22%, respectively (Fig. 2; Appendix S6; $t = -7.4$, $P < 0.01$; $t = -4.1$; $P = 0.02$). Additionally, warming increased total phenolic concentrations in *C. cucullata* by 60% (Fig. 3; Appendix S6; $t = -4.1$, $P = 0.02$) and tended to decrease NDF concentrations (Fig. 4; Appendix S6; $t = 2.9$, $P = 0.07$). Warming impacts on other forage properties of *C. cucullata* and *C. rangiferina* were not statistically significant or near significance following sequential Bonferroni correction (Appendix S6).

In addition, warming tended to alter overall late summer leaf chemistry in *E. vaginatum*, as indicated by differences in PC1 scores ($t = -2.5$; $P = 0.05$). In *E. vaginatum*, warming was associated with an increase in ADF, ADL, P, and phenolics in the ordination (Fig. 1). In the univariate test, warming increased total phenolic concentrations by 38% (Fig. 3; Appendix S6; $t = -4.0$, $P = 0.03$); impacts on all other forage quality properties were not significant in univariate tests (Appendix S6).

Seasonal variation and effects of experimental warming on B. glandulosa *leaf forage quality*

Warming impacts on *B. glandulosa* forage quality throughout the season were variable. First, *B. glandulosa* leaf forage quality varied across the growing season for N and phenolics (Fig. 5; Appendix S7; Date, $F_{5,39} = 55.3$, $P < 0.01$, and $F_{5,39} = 4.3$, $P < 0.01$, respectively), and there was a trend for P concentrations to also vary seasonally (Fig. 5; $F_{5,38} = 2.2$, $P = 0.08$). Warming tended to alter the seasonal pattern in leaf N concentration (Fig. 5a; treatment × date, $F_{5,39} = 2.1$, $P = 0.09$), reducing N concentration in early summer (late June and early July; treatment, $F_{1,7} = 7.5$, $P = 0.03$). Warming tended to increase leaf P concentrations (Fig. 5b; $F_{1,6} = 4.9$, $P = 0.07$), but did not alter their seasonal pattern (i.e., treatment × date not significant; Appendix S7). Although warming appeared to increase P at the end of the season, this effect was not statistically significant across the full

growing season ($t = -1.8$; $P = 0.11$). Last, warming did not alter *B. glandulosa* total phenolic concentrations (Fig. 5c; Appendix S7).

Discussion

Overall impacts of summer warming on Rangifer *forage quality and quantity*

Our results clearly demonstrate that summer warming can significantly alter the nutritional quality of important *Rangifer* forage species in Low Arctic dwarf shrub tundra. These responses represent the cumulative effects after eight years, and were species- and chemistry-specific, with a net increase in forage quality in some species and a clear decrease in others. However, not all species are of equal importance to *Rangifer* diets and protein accretion. Therefore, the overall impact of these findings on *Rangifer* nutrition will be a function of the relative proportions of each species in the *Rangifer* diet, how climate warming affects the abundances of each of those species, and the animals' ability to select and digest forage components according to their nutrient contents and digestibility. The discussion below focuses on *E. vaginatum*, the lichens, and *B. glandulosa*, because these are generally the most important species/growth forms in the diets of migratory tundra *Rangifer* (Appendix S1). Evergreen shrub responses are not discussed since they were minimal and are of less relevance to *Rangifer*.

The greenhouse treatment strongly increased *E. vaginatum* total phenolic concentrations, and had no impact on nutrient concentrations (Figs. 2 and 3), refuting Hypothesis 1 for this species and suggesting that warming may reduce *E. vaginatum* forage quality in late summer. Graminoids are highly productive (20–30% of NPP; Chapin et al. 1995, Zamin et al. 2014), and their growth rates are rapidly stimulated by warming (Elmendorf et al. 2012*a, b*, Doiron et al. 2014, Zamin et al. 2014). Graminoids are most important to *Rangifer* nutrition early and late in the summer when their nitrogen concentration and digestibility are high relative to other species (Appendix S1; Côté 1998, Johnstone et al. 2002). We were only able to test a single graminoid species since it was the only abundant graminoid in our experimental plots. Nonetheless, previous work has shown that warming impacts on nitrogen concentrations were consistent across four graminoid species in a High Arctic site (Doiron et al. 2014).

In contrast to the increase in graminoid forage quantity with warming (Elmendorf et al. 2012*a, b*), the changes in forage quality in *E. vaginatum* imply negative net impacts largely driven by the increased phenolics with warming. By contrast, previous research has shown experimental warming reduced graminoid nitrogen concentrations, which would also translate to decreased forage quality (Aerts et al. 2009, Nybakken et al. 2011, Doiron et al. 2014). Graminoids tend to have much lower phenolic concentrations than shrubs in late summer (e.g., 43 vs. 144 mg/g dry mass at this site;
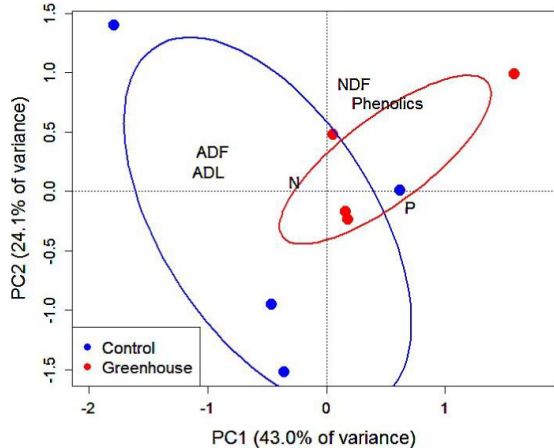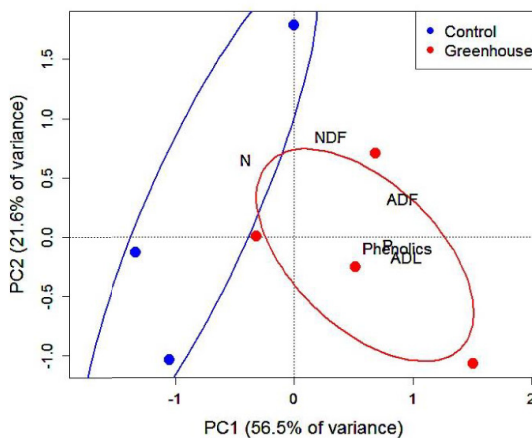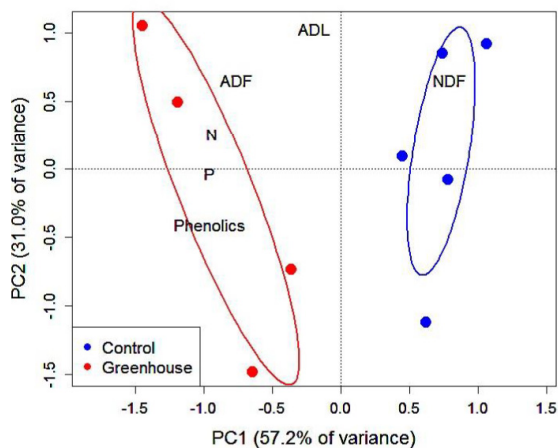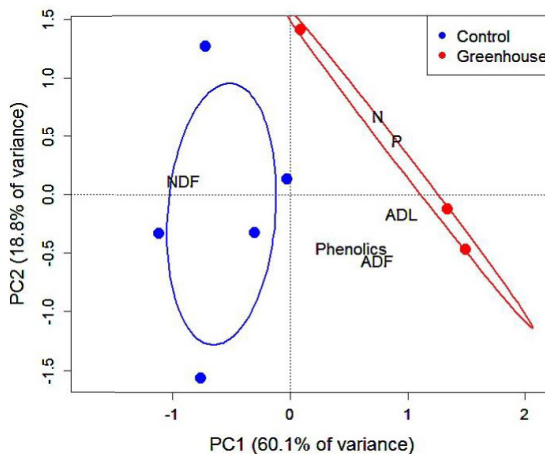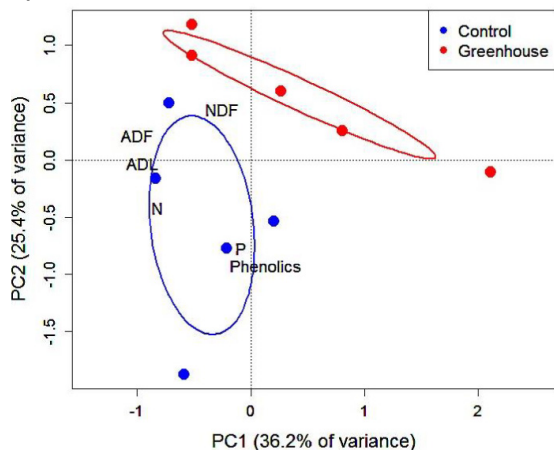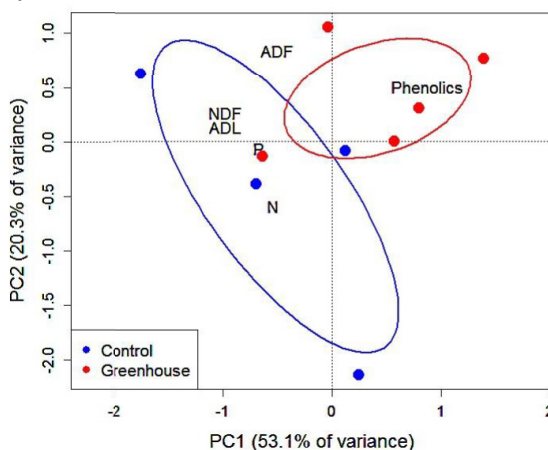
Fig. 1. Principal components analyses of late summer forage chemical properties in (a) a deciduous shrub, (b) graminoid, (c, d) common lichens, and (e, f) evergreen shrubs of the Canadian Low Arctic. PCA scores for each analysis are in Appendix S4 and statistical test results of treatment effects on PC1 scores are in Appendix S5. Ellipses delineate the 95% confidence intervals for the control and greenhouse treatment clusters. Forage properties used in the analyses are neutral-detergent fiber (NDF), acid-detergent fiber (ADF), acid-detergent lignin (ADL), nitrogen (N), phosphorus (P), and total phenolic concentrations.
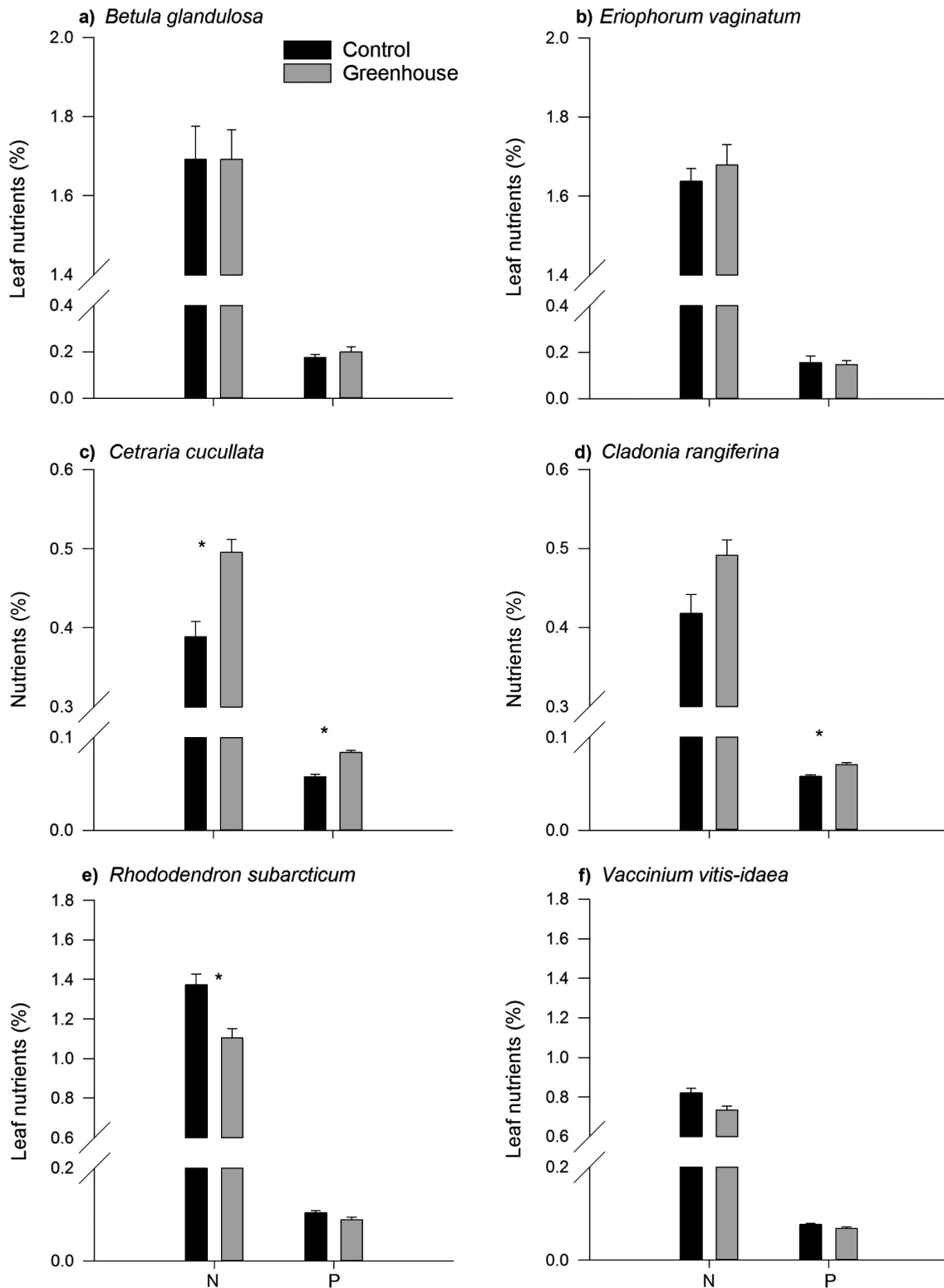
Fig. 2. Effects of greenhouse warming on late summer nitrogen (N) and phosphorus (P) concentrations in (a) a deciduous shrub, (b) graminoid, (c, d) common lichens, and (e, f) evergreen shrubs. Error bars are standard errors ($n = 5$ for all except *E. vaginatum* P concentrations where $n = 4$). Species-level univariate test results are indicated as *$P < 0.05$ following sequential Bonferroni correction. Corresponding statistical test results are in Appendix S6.

Appendices S1 and S8), and similar nitrogen concentrations (Appendices S1 and S8; Zamin and Grogan 2013). Therefore, the large increase (38%) in *E. vaginatum* phenolics with warming may substantially reduce its forage quality. However, such inferences must be treated with caution because forage quality is also influenced by species differences in the protein precipitation capacity of its phenolic compounds (Robbins et al. 1987). Furthermore, these inferences are based on total (i.e., combined) phenolics, although it is well recognized that specific phenolic compounds may have disproportionately large impacts on herbivores (Forbey et al. 2011). Therefore, further analyses of the composition and protein precipitation capacities (Robbins et al. 1987, McArt et al. 2006) of the leaf phenolic compounds of these species are required to fully evaluate the net effects of the involved phenols on forage quality.

The warming impacts on forage quality of the two lichen species, *C. cucullata* and *C. rangiferina*, were particularly complex. Contrary to Hypothesis 1, warming increased N concentrations for both species and P concentrations for *C. cucullata* (Fig. 2), yet also increased total phenolics in *C. cucullata* (Fig. 3). Lichens consistently decline in abundance and biomass with experimental warming at least partly because of the concomitant increase in vascular plant growth and the associated increase in shading and litter (Cornelissen et al. 2001, Elmendorf et al. 2012a, Lang et al. 2012, Zamin et al. 2014). Altogether, the lichen forage quality changes reported here in response to warming, coupled with the biomass reductions cited above, imply negative consequences for *Rangifer* nutrition. The net effect of the observed changes in lichen nutrients and phenolics depends on whether the strong increases in phenolics (1) reduce caribou nutrient absorption during digestion, thereby restricting the benefits of the increased nutrients

in the forage; and (2) reduce total forage intake (Appel 1993). As with *E. vaginatum*, analysis of the phenolic composition of these lichens and of their protein precipitation capacities (Robbins et al. 1987, McArt et al. 2006) will assist in determining the net impact on forage quality. Meanwhile, previous research in alpine southern Norway found different experimental warming impacts on lichen chemistry to those documented here (Nybakken et al. 2011). Specifically, warming did not alter nitrogen concentrations of four lichen species, and decreased concentrations of the phenolic compound usnic acid (Nybakken et al. 2011). The difference in effects may be in part due to the extent of increase in temperature, with the greenhouses used in our study increasing temperatures 2.2°C compared to the 1.5°C of Nybakken et al.'s (2011) open-topped chambers. Carefully designed cross-site studies to determine the full diversity of drivers behind this regional variation in lichen chemical responses, as well as further research on the protein precipitation capacities of the affected phenolics, will be required to enable accurate projection of warming impacts across the ranges of all herds.

Changes in B. glandulosa *forage quality properties over the growing season*

Our phenological data show that warming reduced *B. glandulosa* leaf nitrogen concentrations in spring and early summer (Fig. 5), supporting Hypothesis 2. It is unclear if the nutrient concentrations reported for the first sampling date (June 28) represented the seasonal peak for both treatments, or if the peak had happened in advance of this date in the greenhouse treatment for example. Sampling immediately at the start of leaf emergence rather than 2 weeks later would enable more robust conclusions about warming impacts on peak nutrient concentrations. Nevertheless, the observed treatment effect is clearly important at this critical time for *Rangifer* nutrition.

Despite this decrease in forage quality, the net impact of warming on *B. glandulosa* as *Rangifer* forage could be positive or negative (Boertje 1984, Cornelissen et al. 2007, Christie et al. 2015). Deciduous shrubs are the most important forage plants on the summer range of many *Rangifer* herds, making up from 22% to 77% (mean 45%) of total dietary composition (Appendix S1; Boertje 1984, Witter 2010). Deciduous shrub biomass has been increasing across the Arctic in correlation with recent climate warming trends (Goetz et al. 2005, Tape et al. 2006, Epstein et al. 2012). Meanwhile, increased deciduous shrub abundance will only translate to increased *Rangifer* forage quantity if warming increases biomass of preferred species (Christie et al. 2015), such as is occurring for *B. glandulosa* in the eastern Canadian Arctic (Manseau et al. 1996) and *Salix* spp. in the western North American Arctic (Boertje 1984). In the latter region, *B. glandulosa* may not meet *Rangifer* nitrogen requirements because of its relatively high phenolic
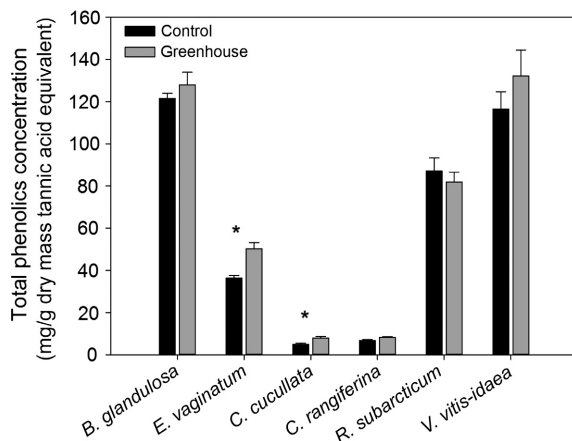

Fig. 3. Effects of greenhouse warming on leaf and lichen phenolic concentrations in late summer. Error bars are standard errors (*n* = 5); Species-level univariate test results are indicated as *P < 0.05 following sequential Bonferroni correction. Corresponding statistical test results are in Appendix S6.
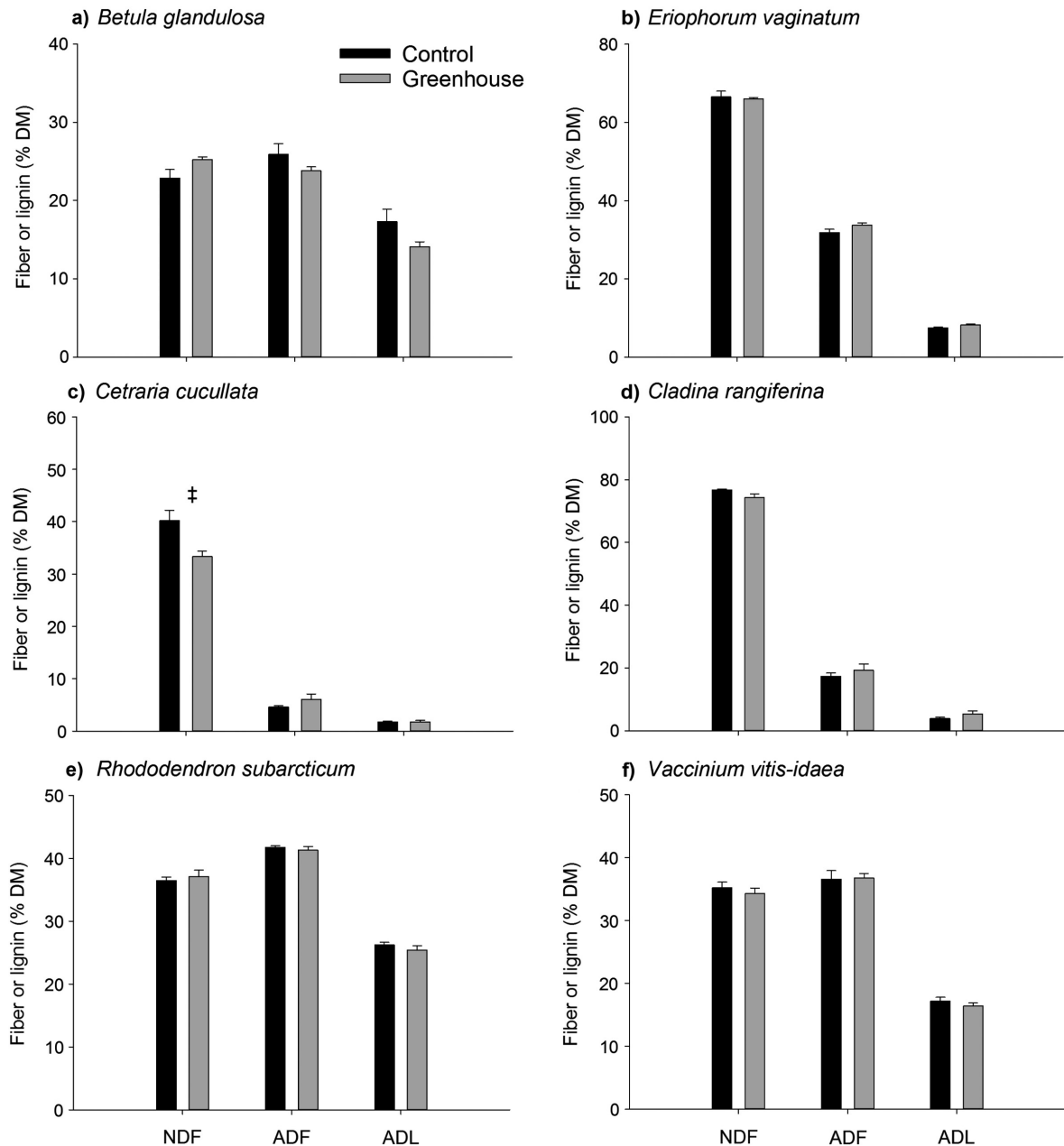
Fig. 4. Effects of greenhouse warming on neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent lignin (ADL) in (a) a deciduous shrub, (b) graminoid, (c, d) common lichens, and (e, f) evergreen shrubs, measured as percent dry mass. All samples were collected in mid-August. Error bars are standard errors (n = 3–5, see table in Appendix S2 for specific sample sizes). Species-level univariate test results are indicated as *P < 0.05, ‡P < 0.10 following sequential Bonferroni correction. Corresponding statistical test results are in Appendix S6.

concentration compared to other forage species (Thompson and Barboza 2014). Furthermore, increased deciduous shrub growth could have a negative impact on *Rangifer* if it leads to dense thickets of shrubs that the animals avoid because of predation risk (Boertje 1984), or indirectly reduces lichen biomass because of shading and canopy litter accumulation (Cornelissen et al. 2001, Lang et al. 2012). Finally, increased snow accumulation

associated with shrubs (Sturm et al. 2005) could increase energy costs for movement (Stuart-Smith et al. 1997) or alter forage availability (Tyler 2010). Altogether, the net impact of increased deciduous shrub growth on the availability of preferred *Rangifer* forage remains unclear.

While warming is likely to increase *B. glandulosa* forage quantity (Zamin et al. 2014), our results indicating a ~10% reduction in leaf N concentrations in late June
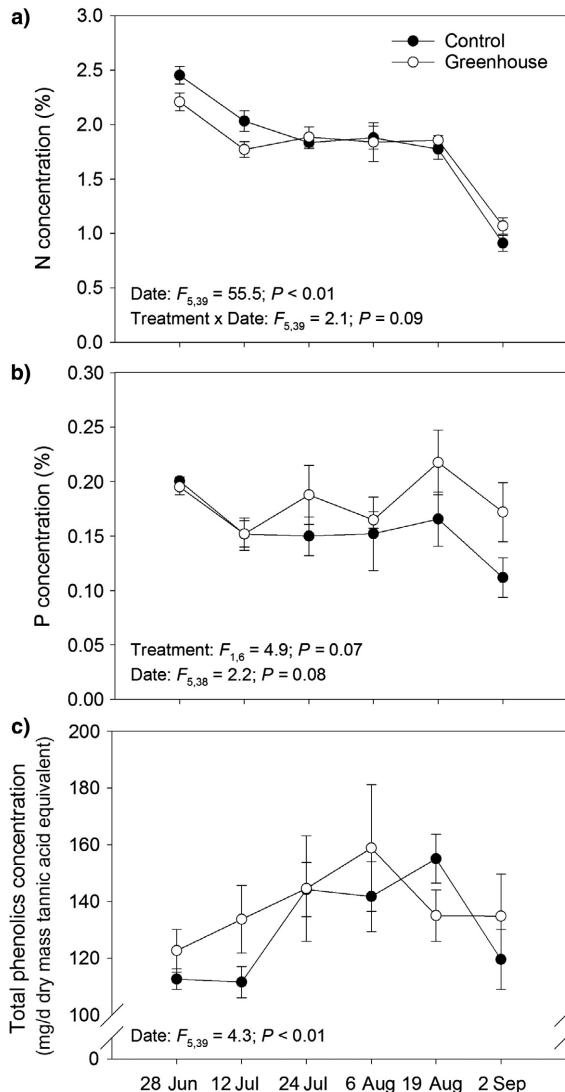
FIG. 5. Effects of greenhouse warming on *B. glandulosa* (a) leaf nitrogen, (b) phosphorus, and (c) phenolic concentrations throughout the growing season. Error bars are standard errors (*n* = 5). Statistical test results in the left corners are for repeated-measures ANOVAs. Corresponding statistical test results are in Appendix S7.

and mid-July strongly suggest that it may decrease early summer *B. glandulosa* forage quality. This forage quality reduction has the potential to negatively affect *Rangifer* body condition because it occurs at a time of high nutrient demand to support lactation (Crête and Huot 1993, Taillon et al. 2013). Poor forage conditions during lactation can increase the depletion of female fat reserves and slow calf growth (Crête and Huot 1993). Moreover, forage quality in early summer affects *Rangifer* body protein in the autumn (Couturier et al. 2009), with inadequate autumn body reserves possibly leading to interrupted gestation and a decline in pregnancy rates (Crête and Huot 1993). However, this potential trophic mismatch may be avoided if the timing of *Rangifer*

migration advances accordingly, which has been observed for some herds (Le Corre 2017), but not others (Post and Forchhammer 2008).

Implications for Rangifer: temporal and spatial adaptability

Several temporal and spatial factors interact to determine *Rangifer* responses to changes in forage quality and quantity within their feeding range. For example, spring weather conditions, snow depth, and snowmelt timing influence the timing of spring migration (Russell et al. 1993, Gunn and Poole 2009, Le Corre et al. 2017). Experimentally advancing the timing of snow melt has led to advanced initiation of plant growth (Starr et al. 2000, Natali et al. 2012), which may shift nutrient phenology (Doiron et al. 2015). In addition, calving ground locations are known to shift in association with changing snow conditions, range quality, timing of plant green-up, and *Rangifer* population size (Gunn et al. 2008, Taillon et al. 2012). The hundreds of kilometers that separate the wintering grounds from the spring calving grounds may result in a trophic mismatch if the environmental changes are not synchronous across the whole migratory range. Meanwhile, *Rangifer* are selective for forage at both the landscape- and vegetation-patch scales (White and Trudell 1980, Skarin et al. 2008), suggesting that they may modify forage selection to utilize the most nutritious species in a given time and space. For example, the warming-induced reductions in forage quality that we observed may cause caribou to decrease their use of *B. glandulosa* in early summer and of *E. vaginatum* in late summer.

The extent to which warming may alter migratory *Rangifer* body condition and population sizes will depend on many concurrent stressors (Festa-Bianchet et al. 2011), including changes in summer forage quality. These changes in forage quality combined with anticipated changes in relative biomass within the mesic tundra vegetation community may have negative impacts on *Rangifer* nutrition in early and late summer. Warming decreased nitrogen concentrations and increased phenolic concentrations during these critical time periods for two important forage species (*B. glandulosa* and *E. vaginatum* respectively), and had mixed effects on two common lichen species. *Rangifer* demonstrate spatial and temporal plasticity in response to changing weather and range conditions, and are very capable of shifting calving ground locations (Gunn and Poole 2009). Nonetheless, it remains unclear as to how the upcoming changes will compare to those previously experienced, and whether *Rangifer* herds can accommodate the rate, direction and magnitude of these changes. The complexity of making predictions on changes in forage abundance and quality is also increased by the variability in the impacts of *Rangifer* themselves on their range (Bernes et al. 2015, Campeau 2016). Altogether, as the Arctic continues to warm, these concerns highlight the importance of conservation strategies that

can accommodate uncertainty and variability (Taillon et al. 2012) to ensure that there is sufficient appropriate habitat available so that *Rangifer* can modify their foraging and range use in a rapidly changing environment.

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