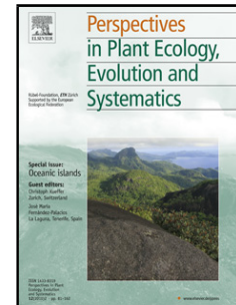


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Gatekeepers to the effects of climate warming? Niche construction restricts plant community changes along a temperature gradient

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Highlights

- ~~Crowberry abundance increases with temperature~~
- ~~Herbaceous plant abundance increases with temperature, but not in communities where crowberry is present~~
- ~~Reindeer promote abundance of the crowberry plant, but not of its berries~~
- ~~Niche construction by crowberry is likely to modify effects of climate change in tundra ecosystems~~

Abstract

Organisms that modify the environment (niche constructors) are likely candidates to mediate the effects of climate warming. Here we assess tundra plant community changes along a temperature gradient and how these are modified in the presence of the common allelopathic dwarf shrub *Empetrum nigrum* and the large herbivore *Rangifer tarandus*.

We developed a structural equation model based on data from a field-based study of 1450 tundra plant communities across Northern Fennoscandia, covering a temperature gradient of 3.5°C, contrasting *Rangifer* densities, a range of *Empetrum* abundances in addition to gradients in topography and bedrock.

We found temperature to be a significant positive predictor of *Empetrum*, herbaceous and woody plant abundances. However, the effect of temperature as predictor for herbaceous plant abundance was significantly reduced in communities with *Empetrum* present. For woody plant abundance *Empetrum* was a stronger predictor than temperature. In comparison, we found *Rangifer* density to have marginal or no effect on either herbaceous or woody plant abundance. These findings were not modified by either topography or bedrock.

Results from this study indicate that herbaceous plant responses to climate warming are currently reduced in communities where *Empetrum* is present, whereas the abundance of *Empetrum* and other woody plants is promoted. Results also indicate that any future *Empetrum* encroachment is likely to drive tundra communities towards slower process rates and lower biodiversity. As such our results substantiate the importance of understanding the dynamics of niche constructor species and include them in predictive models of climate change.

Key words

Empetrum nigrum, *Rangifer tarandus*, herbaceous plants, structural equation model, niche construction, ecosystem engineering

Introduction

The tundra is changing (e.g. Chapin *et al.*, 2005, Elmendorf *et al.*, 2012b, Wookey *et al.*, 2009), with the potential to become more species rich and greener under climate warming (e.g. Aerts *et al.*, 2006, Epstein *et al.*, 2012, Kullman, 2010, Rustad *et al.*, 2001).

Environmental modification by organisms, also termed niche construction or ecosystem engineering (Odling-Smee *et al.*, 2013), may, however modify effects of climate warming. Plants can modify the environment in tundra plant communities, for instance by changing nutrient cycling rates (Bråthen & Ravolainen, 2015), subsequently causing plant-based cascade processes that enhance or reduce responses to climate change (Wookey *et al.*, 2009). In addition, herbivores can counteract the greening process (shrub encroachment into circumpolar or alpine areas) (den Herder *et al.*, 2008, Olofsson *et al.*, 2009, Post, 2013, Ravolainen *et al.*, 2014, Zamin & Grogan, 2013), and hence prevent plant-based cascade processes. The trajectory of change under climate warming may therefore be dependent on the niche constructing abilities of plants and herbivores inhabiting the tundra.

Plant species are tracking their temperature niche as indicated by the upward and northward changes in species distributions in response to a warming climate (Chen *et al.*, 2011, Klanderud & Birks, 2003, Lenoir *et al.*, 2008). A thermophilization of the tundra flora is happening, where warm adapted species replace cold adapted species (Elmendorf *et al.*, 2015, Gottfried *et al.*, 2012). Because warm adapted species are benefited under climate warming and because the species richness is larger among warm adapted species, an increase in species richness is expected (Kullman, 2010). Yet, at the plot scale, no significant increase in species richness has happened in tundra areas in 30 years, whereas there have been changes in the height and abundance of growth forms (Elmendorf *et al.*, 2012b) with increases described for shrubs, graminoids and forbs (Elmendorf *et al.*, 2012a). Shrubs, in particular, are already common in tundra ecosystems (Walker *et al.*, 2005), and are increasing with recent observed climate warming (Elmendorf *et al.*, 2012b, Myers-Smith *et al.*, 2011). However, how this increase in shrub dominance is linked to community species richness and abundance of other growth forms is not evident. Theoretically, shrub encroachment can cause a range of possible outcomes for plant communities depending on the ecological context (Wookey *et al.*, 2009) and empirical evidence of decreasing (Klein *et al.*, 2004, Mod *et al.*, 2016, Post, 2013, Wilson & Nilsson, 2009), stable (Pajunen *et al.*, 2011) and increasing (Bråthen & Lortie, 2016) species richness of vascular plants as a response to shrub encroachment has been found. To advance in the understanding of how ecological contexts influence responses of plant

communities to climate warming, large-scale studies on dominant shrub species within a range of habitats and contexts are needed (Christie *et al.*, 2015).

The evergreen dwarf-shrub *Empetrum nigrum* (crowberry) has strong niche constructing capacity (*sensu* Matthews *et al.*, 2014) as indicated by its ability to modify ecosystem properties (Bråthen & Lortie, 2016, Nilsson & Wardle, 2005, Tybirk *et al.*, 2000, Wardle *et al.*, 1998). *Empetrum* is tightly linked to variation in species diversity of tundra plant communities under both high and low intensity *Rangifer tarandus* (reindeer) land use (Ravolainen *et al.*, 2010). The abundance of *Empetrum* has repeatedly been found negatively related to species richness of vascular plants in tundra communities (Bråthen & Lortie, 2016, Bråthen & Ravolainen, 2015, Mod *et al.*, 2016, Wilson & Nilsson, 2009). Accordingly, *Empetrum* is found to be an important predictor along with temperature in species distribution models (Pellissier *et al.*, 2010) and in plant community models (le Roux *et al.*, 2014). However, although allelopathic to other plant species at their seedling state (González *et al.*, 2015), *Empetrum* does not always have negative effect on coexisting plants. Whereas *Empetrum* is competitively superior to forb and grass species (Mod *et al.*, 2014, Pellissier *et al.*, 2010, Wilson & Nilsson, 2009), it can have facilitative effects for species with higher leaf dry matter content (Mod *et al.*, 2014, Pellissier *et al.*, 2010). *Empetrum* may thus modify the environment, thereby driving selection for species with traits causing slow nutrient process rates (cf. Wilson *et al.*, 1999), and potentially reinforcing the filtering effect that *Empetrum* has on the species pool. This is especially pertinent to herbaceous species in tundra plant communities.

Dendroecological studies indicate *Empetrum* is sensitive to climate change (Buntgen *et al.*, 2015, Myers-Smith *et al.*, 2015), and empirical evidence indicates that *Empetrum* is advancing in altitude and abundance in tundra areas in response to recent climate warming (Felde *et al.*, 2012, Klanderud & Birks, 2003, Wilson & Nilsson, 2009). Such observations of a positive response to warming are corroborated by experiments (Buizer *et al.*, 2012, Kaarlejärvi *et al.*, 2012, Wada *et al.*, 2002), and indicate shrub encroachment by *Empetrum* is promoted by climate warming. However, *Empetrum* has been found to be vulnerable to extreme climatic events during winter (Bokhorst *et al.*, 2008) and to attacks

by the *Empetrum*-specific parasitic fungus *Arwidssonia empetri* under increased snow cover (Olofsson *et al.*, 2011). Still, *Empetrum* has been found resilient to simulated strong winter damage (Aerts, 2010), has a high tolerance to ice encasement (Preece *et al.*, 2012, Preece & Phoenix, 2014), and it appears that *Empetrum* is relatively resistant to a range of environmental changes, including fertilization, as compared to coexisting species (Tybirk *et al.*, 2000). Hence, although *Empetrum* has been found to be vulnerable to some aspects of climate warming, it seems it mostly thrives.

Empetrum abundance is also affected by herbivores. For instance, close to fences that separate *Rangifer* migration areas, trampling can be intense (Moen & Danell, 2003). As *Empetrum* is vulnerable to trampling (Bell & Tallis, 1973), this can result in reduced abundance (Olofsson *et al.*, 2001, Väisänen *et al.*, 2014). Small rodents have also been shown to control *Empetrum* abundance (Olofsson *et al.*, 2009, Olofsson *et al.*, 2012), but a longer time collapse in small rodent cycles (Ims *et al.*, 2008), may have reduced the capacity of small rodents to do so. Furthermore, while most studies indicate that herbivory are counteracting the encroachment of shrub species, there are empirical indications of *Empetrum* responding differently and that it is rather promoted by *Rangifer* activities (Bråthen *et al.*, 2007b, Francini *et al.*, 2014, Yläne *et al.*, 2015). Such promotion potentially happen through apparent competition because *Empetrum* leaves have low palatability (Tybirk *et al.*, 2000) and through endozoochory because *Empetrum* berries are eaten by e.g. *Rangifer* (Bråthen *et al.*, 2007a). Hence, *Empetrum* seems to be both positively and negatively affected by the activities of herbivores.

In sum, an assessment of how *Empetrum* itself is affected by increasing temperatures and *Rangifer* density, and how *Empetrum* affects tundra plant communities in this context, is likely to yield insight into the development of tundra plant communities under climate warming. Therefore, in this study, we ask to what extent *Empetrum* and *Rangifer* are likely candidates for mediating effects of climate warming in tundra plant communities. We use a space for time approach to address climate warming effects (Blois *et al.*, 2013, Elmendorf *et al.*, 2015): the study design cover a temperature gradient of 3.5°C across a total of 1450 randomly chosen tundra plant communities in the Fennoscandian part of the circumpolar dwarf shrub tundra (*sensu* Walker *et al.*, 2005). The communities are defined

as where plant species share a habitat or environment (*sensu* Daubenmire, 1968). *Empetrum* varies in abundance across these communities, from being absent to subordinate and to having supreme dominance. The study design concomitantly covers ten district pairs of high vs. low intensity of *Rangifer* husbandry land use, and has previously been used to assess effects of *Rangifer* density on the ecosystem state of the tundra communities (Bråthen *et al.*, 2007b), focusing on mammalian herbivore abundances (Ims *et al.*, 2007) and plant diversity (Bråthen & Lortie, 2016, Bråthen & Ravolainen, 2015). In this study we hypothesize that (1) *Empetrum* abundance increases along the temperature gradient, and that (2) higher *Rangifer* densities promote *Empetrum* abundance at higher temperatures. We also hypothesize that (3) *Empetrum* reduces the effect that increasing temperatures has in promoting both inflorescences and biomass of growth forms with higher process rates such as forbs and grasses. In addition, since higher *Rangifer* densities have already been shown to reduce biomass of forbs and grasses as well as the abundance of inflorescences (Bråthen *et al.*, 2007b), we hypothesize that (4) *Rangifer* counteract any positive effect of temperature on the abundance of herbaceous plants. Furthermore we hypothesize that (5) *Empetrum* and increasing temperatures facilitate the biomass of other shrub species, but that (6) higher *Rangifer* densities do not modify this relationship because the abundance of these growth forms is mostly independent of *Rangifer* densities (Bråthen *et al.*, 2007b). In order to test these hypotheses in a comprehensive way we developed a structural equation model, and then we tested each hypothesis separately.

Materials and methods

Study area

Field work for this study was conducted in the coastal alpine tundra of northern Fennoscandia between latitudes 69.2-71.2°N and longitudes 20.5-31.3°E (Fig. 1). This is a region characterized primarily as dwarf-shrub tundra (Walker *et al.*, 2005), with *Empetrum nigrum* being both the most common shrub and the most dominant plant (Bråthen *et al.*, 2007b, Ravolainen *et al.*, 2010). The region is typically snow covered until late June and the main vegetation types are heath, meadows and marshes. Besides *Empetrum*, heath is dominated by the dwarf shrubs *Betula nana*, *Salix herbacea*,

Vaccinium myrtillus, *V. vitis-idaea* and *V. uliginosum*. Forb and grass-rich meadows are often populated with *Bistorta vivipara* and *Viola biflora*, *Avenella flexuosa*, *Deschampsia cespitosa*, *Anthoxanthum nipponicum*, and sedges of *Carex* spp. Marshes are dominated by *Eriophorum angustifolium* and *E. vaginatum* along with various species of *Carex*. *Empetrum* is often present in both meadows and marshes. Plant names follow the Pan-Arctic Flora (<http://nhm2.uio.no/paf/>). The main large herbivores in this region are the migratory, semi-domestic *Rangifer tarandus* that have their summer pastures along the coast, which is divided into districts to facilitate management. Other common herbivores include moose (*Alces alces*), domestic sheep (*Ovis aries*), and small rodents (Ims *et al.*, 2007).

The study region is characterized by steep climatic gradients from west to east as well as from coast to inland, caused by the warm NE Atlantic Current that gradually declines from west to east (see temperature map in Fig. 1). The northernmost coast of the study region is classified as Arctic (Walker *et al.*, 2005). Average summer precipitation (June, July and August) is 65, 54 and 48 mm in the west, middle, and east of Finnmark, respectively (calculated from Norwegian Meteorological Institute, <http://www.eklima.no>). The coastal part of the study region is furthermore characterized by variable bedrock (mainly gabbro in the west, slate and sandstone towards the east [Geological Survey of Norway, <http://www.ngu.no/>]).

Study design

A total of 1450 plant communities were sampled within the borders of ten pairs of neighbouring *Rangifer* districts (Fig. 2), where each pair represent two decades of high versus low *Rangifer* densities (official numbers provided by the Norwegian Reindeer Husbandry Administration <http://www.reindrift.no/>) (Bråthen *et al.*, 2007b). Different *Rangifer* densities are to a large extent determined by spatiotemporally heterogeneous management practices in *Rangifer* husbandry (Tveraa *et al.*, 2007). Faeces counts in the field confirmed that each pair of neighbouring *Rangifer* districts represented a contrast in low and high *Rangifer* density (Bråthen *et al.*, 2007b).

Sampling within the *Rangifer* districts was based on *a priori* stratification and plant

community selection using GIS as well as on rules set *a priori* to the field sampling (*sensu* Mörsdorf *et al.*, 2015). Each *Rangifer* district was covered with a 2 x 2 km grid (in which each cell is referred to as a “landscape area”). For each district, and in order to avoid landscape areas dominated by glaciers, lakes and boulder fields, satellite image classifications of vegetation types (Johansen *et al.*, 1995) were evaluated to identify landscape areas with more than the district average of mesic and wet vegetation. Among these, landscape areas were retained unless they included >50% forest, lakes, sea, glaciers or included a fence or a major road (based on <http://www.norgeskart.no/>). The final landscape areas within each *Rangifer* district were selected randomly. The number of selected landscape areas increased as a function of district area, with the final number of selected landscape areas per district ranging from 6 to 14 units.

The choice of plant communities within the selected landscape areas was random. The landscape areas were subdivided into 100 potential sampling squares of 200 m x 200 m, with a maximum of 25 randomly selected squares (Fig. 1). The centre of each selected square was the starting position for a 50 m long transect whose direction was determined by a random GPS position on a circle with a 50 m radius. If any of the transects had to be discarded because of steep terrain, water (lake, large river or very wet mire), snow cover (more than a 5 m section of the transect running through snow), boulder field (more than half of the transect running over boulders devoid of vegetation), or the transect was below the tree-line, another random direction or start position was identified. If no new acceptable transect placement within the area was available, the entire sampling square was discarded. Each transect was sub-sampled at plots every 5 m along the transect with a triangular sampling frame with sides of 40 cm. Each transect constituted a tundra plant community (Fig. 1). All landscape areas were sampled in July and August 2003. Each landscape area was sampled by two individuals but for a few areas sampled by one person. To avoid differences due to plant phenology, *Rangifer* districts belonging to the same pair were analysed simultaneously, and sampling was conducted from west to east as the season progressed in order to sample at or just after peak growing season.

Environmental variables

A downscaled WorldClim temperature layer ("Warmest Quarter" Hijmans *et al.*, 2005) of

100 m x 100 m resolution (Pellissier *et al.*, 2013) was applied for average summer temperatures (Fig. 1). We used average summer temperature (across June, July and August) because it is physiologically more meaningful to alpine species than other temperature variables (Körner, 2003).

Bedrock types for each plant community were obtained from maps provided by the Geological Survey of Norway (<http://www.ngu.no/>). The bedrock type was classified as poor (0), e.g. quartzite, moderate (1) e.g. amphibolite, and rich (2) e.g. mica or limestone, in providing nutrients available to the plant community as based on Tarbuck and Lutgens (1992).

A curvature index, i.e. a geodaphic factor that serves as a surrogate for the moisture level of vegetation (Moore *et al.*, 1991), was calculated per plant community using GIS and a digital terrain model of 25 m x 25 m pixels (<http://www.kartverket.no>). Index values from 1 to -1 indicate concave to convex curvature, i.e. moist to dry terrain, respectively. Visual inspection in the field of a few sites verified that the index values correctly depicted concave or convex terrain.

Biological variables

In each plot the point intercept method (Bråthen & Hagberg, 2004) - using three pins attached to the corner of the triangle (Fig. 1) - was used to obtain measures of above ground live vascular plant species biomass. Prior to further analyses, point intercept data per species and plot were converted to biomass estimates in units of grams per m² using established calibrations (Ravolainen *et al.*, 2010). To achieve estimates of growth form biomasses and total biomass per plant community, the data were summed across species and averaged across all plots. Point intercept data on inflorescences (including all inflorescence parts and all their phenological stages) were registered separately, and were summed across species and averaged across all plots to achieve estimates of inflorescences abundance per plant community. Estimates of *Empetrum* biomass and *Empetrum* berry abundance were calculated separately.

Data analyses

Structural equation models were developed in the R environment version 3.2.3

(<http://www.r-project.org>) using in the lavaan package (Rosseel *et al.*, 2013). Data were screened for distributional properties and nonlinear relations which resulted in several variables being log-transformed. The first structural equation model was exploratory, built to test the effect of all predictor variables (temperature, *Rangifer* density, curvature and bedrock) onto the abundance of herbaceous and woody growth forms. The possible mediating effect by the abundance of *Empetrum* was included in the model by having *Empetrum* both as a response variable and as a predictor to the plant growth form abundances. All non-significant predictors were successively removed from the model. The final model was selected based on parsimoniousness and goodness of fit as interpreted from Chi Square tests, RMSEA and Comparative Fit Index provided in the lavaan package (Rosseel *et al.*, 2013). The contribution of each predictor variable in the final model was then assessed in order to possibly simplify the model further. Final models with one predictor variable removed at a time were compared to the final model using anova model comparison. The final model including all predictors had the best AIC score. Lastly, the final model was tested for whether the hierarchical setup of the study design had any consequences to the variance explained by the model using the lavaan survey package and by an assessment of the robust Chi Square test (Oberski, 2014). At this stage, all predictors were retained in the model, including predictors that became non statistically significant but still explained variance above a value of 0.04. Variance explained by the different predictor variables was obtained from model outputs as standardized values, and manually entered into a path diagram of the final structural equation model.

In addition we developed linear mixed effects models (Pinheiro & Bates, 2000) using the nlme package in R to test specific hypotheses. In the first set of models fixed factors were *Empetrum* biomass and *Empetrum* berries as response variables and temperature and *Rangifer* density (high and low) as predictor variables. For the model on *Empetrum* berries *Empetrum* biomass was also a predictor. In a second set of models fixed factors were species richness, the abundance of inflorescences, and the biomass of each growth form as response variables along with temperature, *Empetrum* biomass and *Rangifer* density as predictor variables. For all models the random factors were landscape areas nested in pairs of *Rangifer* districts.

To achieve homogeneity of the residual variance of models, all abundance variables (i.e. inflorescence abundances and biomasses) were log transformed ($x+1$). All predictor variables were standardized (mean=0 and standard deviation=1) to facilitate comparison between variables and models (e.g. Iversen *et al.*, 2014).

The standardized coefficients and the confidence intervals of fixed predictors were extracted from model outputs and presented and plotted as predicted values. From the second set of models the predicted values were presented in three different plant community categories; in communities with *Empetrum* biomass constituting 0%, 20-30% or 70-80% out of total community biomass.

All models were extended with nutrient availability (bedrock index) and moisture level (curvature index) as fixed factors to assess any confounding towards main predictors and are presented with their standardized coefficients in supplementary information (Table S1). In addition, standard deviations and confidence intervals of the random factors for each set of models are presented.

Results

Empetrum was present in 1230 out of the 1450 randomly chosen tundra plant communities, and composed more than half the biomass across all communities. Among the growth forms, forbs constituted on average the least biomass, followed by sedges, grasses, evergreen shrubs (excluding *Empetrum*) and deciduous shrubs (Table 1). In the communities where *Empetrum* was not present, other shrubs constituted on average 55% of the community biomass.

The structural equation modelling (SEM) showed a significant influence of temperature on the biomass of *Empetrum* and herbaceous plants and a non-significant influence on woody plant biomass (Fig. 2). The influence of *Rangifer* density on either response variable was not significant. The influence by *Empetrum* on herbaceous and woody plant biomass was stronger than that of temperature, but with a negative and a positive relationship respectively. Moreover, there was a significant negative interaction between temperature and *Empetrum* on herbaceous plant biomass, indicating the influence of

Empetrum was more negative at higher temperatures. Moisture, as presented in the form of the curvature index, had a significant negative influence on *Empetrum* biomass and a significant positive influence on herbaceous plant biomass. Nutrient availability, as presented by the bedrock index, was only influential to herbaceous plant biomass, and in a positive way.

The bivariate model (linear mixed model) result on the influence of temperature on the *Empetrum* biomass was consistent with the SEM results, showing a marked increase in *Empetrum* biomass in response to increasing temperature (Fig. 3, Table 2). However, in contrast to the SEM results, higher *Rangifer* density had significant positive effect on the *Empetrum* biomass in the bivariate model, but with small effect size (Fig. 3, Table 2). The abundance of *Empetrum* berries was only modelled using a bivariate model, with model results showing slightly less berries in communities with high *Rangifer* densities (Fig. 3, Table 2), and a positive relationship with temperature where also the biomass of *Empetrum* was higher (Table 2).

The bivariate model results on the influence of temperature and *Rangifer* on the biomass of the herbaceous and woody growth forms were also mostly consistent with the SEM results; Temperature had a significant positive relationship with both herbaceous and woody plant biomass whereas the effect of *Rangifer* density was insignificant (Fig. 2, Table 2). With increasing biomass of *Empetrum* in the plant communities these positive relationships to increasing temperature were severely reduced for the herbaceous plant biomass, whereas they were enhanced for the woody plant biomass (Fig. 4a, Table 2). This latter interaction effect on woody plant biomass was however not part of the final SEM model (Fig. 2) because the variance explained by the interaction was less than 0.03.

Bivariate models were run to assess responses among the different herbaceous or woody growth forms. The biomass of each of the growth forms were all significantly positively related to the temperature gradient from 4.4 - 7.9 °C (Fig. 4a, Table 2). The effect of *Rangifer* was insignificant for all growth forms except for forbs and grasses where a negative effect of high *Rangifer* densities was similar in effect size and sign to that of *Empetrum* biomass (Table 2).

The bivariate model on the abundance of inflorescences (not including *Empetrum* inflorescences) showed a similar outcome to that of the forbs and grasses, with a positive effect of temperature, a negative effect of *Empetrum* biomass and a negative effect of high *Rangifer* densities (Fig. 4b). The bivariate model on species richness showed a positive effect of temperature and a negative effect of *Empetrum*, but no effect of different *Rangifer* densities (Fig. 4b, Table 2).

The predictor strength and direction of temperature, *Empetrum* biomass and *Rangifer* density was only slightly modified by adding nutrient availability (i.e. bedrock index) and moisture (i.e. curvature index) as predictors of community characteristics (Table S1). This indicates there were no confounding effects between main predictors and the additional environmental predictors, and is consistent with the SEM results that showed temperature and *Empetrum* biomass had a clear influence alongside that of the environmental predictors. Such lack of confounding is also strengthened by the fact that the full range of moisture and nutrient availability regimes were present in all categories of *Empetrum* dominance (Fig. S1 and S2). Nonetheless, the nutrient availability was significantly positively related to species richness, herbaceous and woody shrub biomass. Moisture was significantly negatively related to *Empetrum* biomass (indicating more *Empetrum* in convex and hence drier terrain) and significantly positively related to species richness, inflorescence abundance and herbaceous biomass (indicating higher abundances in more concave and hence moister terrain).

Discussion

In this study, we assessed the extent to which *Empetrum nigrum* and *Rangifer tarandus*, two species with niche constructing abilities (*sensu* Matthews *et al.*, 2014, Odling-Smee *et al.*, 2013), mediate the response of tundra plant communities to increasing temperatures. We found *Empetrum* - a common dwarf shrub species in circumboreal-polar areas (<http://nhm2.uio.no/paf/>) - to have clear mediating effects whereas we found effects of *Rangifer* - the dominant large herbivore in this ecosystem (Huntington, 2013) - to have no or low mediating effects in comparison. Moreover, we found the biomass of *Empetrum* to be positively affected by increasing temperatures and to be slightly

positively affected by higher *Rangifer* densities. Because *Empetrum* has allelopathic capacity its proliferation implies a deterioration of habitats to a range of other organisms (Aerts, 2010, Bråthen *et al.*, 2010, Nilsson *et al.*, 1993, Nilsson & Zackrisson, 1992, Wallstedt *et al.*, 2001), with potential wide-reaching consequences to circumpolar areas.

Empetrum abundance increases with increasing temperatures

The increase in abundance of both biomass and berries of *Empetrum* with increasing temperatures is in line with previous studies assessing *Empetrum* biomass (Felde *et al.*, 2012, Kaarlejärvi *et al.*, 2012, Klanderud & Birks, 2003, Wada *et al.*, 2002, Wilson & Nilsson, 2009) and reproduction (Buizer *et al.*, 2012). The ability of *Empetrum* to acquire nitrogen early in the season (Larsen *et al.*, 2012, Wipf, 2010) may give it a competitive advantage over other plant species when responding to increasing temperatures. Also, the increase in berry abundance likely contributes to increased establishment and hence increased abundance of *Empetrum* under warmer temperatures. Increase in *Empetrum* abundance with warming has been found along a temperature gradient ranging from 5-15°C (Buizer *et al.*, 2012) (i.e. at higher temperatures than that provided in the current study), indicating climate warming can promote encroachment by *Empetrum* in ecosystems also beyond circumpolar regions.

Higher intensity land use by *Rangifer* husbandry had a marginally positive effect on the biomass of *Empetrum*, and is consistent with previous findings (cf. Bråthen *et al.*, 2007b). The positive effect of *Rangifer* herbivory might have parallels to *Empetrum rubrum*, a species found in the southern hemisphere and with a high genetic similarity to *Empetrum nigrum* (Popp *et al.*, 2011). Claims are that grazing by sheep over the last 100 years has turned grasslands into *Empetrum rubrum* dominated heathlands (Collantes *et al.*, 1999). In our system, the process by which herbivory causes *Empetrum nigrum* to gain abundance on behalf of other species is most likely apparent competition because it has both low nutrient content (Kaarlejärvi *et al.*, 2012, Sorensen *et al.*, 2008), phenolic rich leaves (Gallet *et al.*, 1999, Väisänen *et al.*, 2013) and low palatability (Tybirk *et al.*, 2000) even during winter when food resources are scarce (Danell *et al.*, 1994). *Empetrum* has also been found to benefit from endozoochory by *Rangifer* (Bråthen *et al.*, 2007a). Hence, the reduced abundance of *Empetrum* berries at higher *Rangifer* densities may

ultimately be part of the positive effect of *Rangifer* densities on *Empetrum* abundance: *Rangifer* is likely dispersing *Empetrum* into new habitats. Areas of high *Empetrum* cover are, however, avoided by *Rangifer* (Iversen *et al.*, 2014) and presence of other herbivores is also negatively linked to areas of high *Empetrum* abundance (as shown in a companion study by Ims *et al.*, 2007). There may thus be a threshold in *Empetrum* abundance at which herbivores are no longer influencing its abundance.

Climate warming effects on tundra plant communities modified by Empetrum

Our finding that the abundances of both inflorescences and biomass of herbaceous and woody plants increased with increasing temperatures in the tundra plant communities is in line with expectations of an increase in ecosystem process rates in response to climate warming (Elmendorf *et al.*, 2012a). Increased biomass in general indicates higher productivity. Also an increase in the abundance of inflorescences will likely improve seed availability and new plant establishment because tundra communities often are seed limited (Graae *et al.*, 2011). The biomass of herbaceous plants, the most productive and palatable growth forms (Chapin *et al.*, 1996, Cornelissen *et al.*, 2004, Cornelissen *et al.*, 2007), were more positively related to the increasing temperatures than that of shrubs. However, in communities with *Empetrum* present the strength of temperature as a predictor of higher herbaceous biomass clearly declined. Although herbaceous growth forms utilize different nutrient pools than *Empetrum* (Michelsen *et al.*, 1996), suggesting low direct competition for nutrients, reduced biomass of herbaceous species in the presence of *Empetrum* is likely. That is, recalcitrant evergreen litter can slow warming-induced increases in soil fertility (De Long *et al.*, 2016, Hobbie, 1992). Additionally, forbs and grasses are especially vulnerable to the allelopathic capacity of *Empetrum* at their germination and seedling stage (Bråthen *et al.*, 2010, González *et al.*, 2015). It is thus likely that niche construction by *Empetrum*, through modifying habitat quality for herbaceous plants, limits the capacity of herbaceous plants in tundra communities to respond positively to climate warming.

In contrast, the biomass of woody plants, i.e. dwarf shrubs, was positively related to *Empetrum* biomass. Increases in the abundance of shrub species alongside increases in *Empetrum* have been shown in previous climate warming studies in dwarf shrub heaths

(Buizer *et al.*, 2012, Kaarlejärvi *et al.*, 2012, Wada *et al.*, 2002). Because shrub species in average are long-lived (e.g. Büntgen *et al.*, 2015), they are likely to be promoted by climate warming at an established developmental stage and are hence not as dependent on the seedling stage previously shown to be vulnerable to *Empetrum* interference (González *et al.*, 2015, Nilsson & Zackrisson, 1992). It may rather be that facilitating effects such as sheltering among established shrubs (Wipf *et al.*, 2006) promote shrub species to further encroach upon the tundra in response to climate warming.

Climate warming effects on tundra plant communities modified by Rangifer

The effects of land use by *Rangifer* husbandry on herbaceous growth forms were on average small in comparison to that of *Empetrum*, but when addressing the herbaceous growth forms individually, both forbs and grasses were found to be negatively affected by both higher *Rangifer* densities and *Empetrum* biomass. Hence, our study support studies addressing *Rangifer* grazing where a general reduction of forbs (Bernes *et al.*, 2015), a general decline in seed production (González *et al.*, 2010) and a decrease in the forb response to climate warming (Kaarlejärvi *et al.*, 2013), have been found.

Implications for ecosystem functioning

Niche construction by *Empetrum* can be so strong that the physical removal of the plant itself has no consequence to aboveground species composition or soil abiotic and biotic properties of its habitat even after ten years (Wardle *et al.*, 2012, Wardle & Jonsson, 2013). Such a legacy effect of *Empetrum* niche construction is plausible due to the bioactivity of leaves accumulated in soil (Bråthen *et al.*, 2010, Wallstedt *et al.*, 2005). *Empetrum* may also have cascading effects on plant-herbivore interactions in tundra ecosystems. For instance, the diet of small rodents consists to a large extent of forbs and grasses (Soininen *et al.*, 2013a, Soininen *et al.*, 2013b), which, as shown in this study, have lower abundance in the presence of *Empetrum*. Also, the reduction of forb and grass biomass at higher *Rangifer* densities (Bråthen *et al.*, 2007b) may come as a consequence of *Empetrum* being a dominant species in most plant communities: The relative grazing pressure on forbs and grasses probably increases when co-occurring with *Empetrum*. Critiques of the ecological sustainability of reindeer husbandry (Moen & Danell, 2003) may thus be valid if they are linked to a trajectory of niche construction by *Empetrum*,

promoted by climate warming and more intense *Rangifer* land use, as it may have subsequent cascading effects onto the whole ecosystem.

Implications for model predictions

Shrub expansion following warming in the Arctic is linked to plant longevity and persistence indicating that model assumptions of fast response rates to climate warming are overestimated (Büntgen *et al.*, 2015). The identified linkages between shrub expansion and *Empetrum* and *Rangifer* in this study further indicate that model assumptions of climate responses may be overestimated for areas where species with niche constructing capacity are common. *Empetrum* and to some extent *Rangifer*, as results of this study may indicate, improve niches for long-lived shrubs and deteriorate niches for herbaceous plants. In consequence plant longevity and persistence are favoured over higher process rates and short reaction time to climate warming. Such niche construction may also limit the range expansions of southern species into circumpolar areas (Virtanen *et al.*, 2010) as tundra communities will be less suited as stepping-stones to plants tracking their climatic niche. Accordingly, there is lower variability in warm thermal limits in Fennoscandia as opposed to the Alps, as shown for the climatic niches of species common to the Alps and Fennoscandia (Pellissier *et al.*, 2013). Also, whereas the current assessment of the Arctic acknowledges a controlling impact of herbivores on the encroachment of shrubs under climate warming (Ims *et al.*, 2013), our study shows that the encroachment of a particular shrub, i.e. *Empetrum*, is more likely enforced, although marginally, by herbivory. As such this study substantiate the call for species specific studies on shrub encroachment (Myers-Smith *et al.*, 2011) and further substantiates the conclusion of previous studies to include *Empetrum* (le Roux *et al.*, 2014, Pellissier *et al.*, 2010) and *Rangifer* (Ims *et al.*, 2013) into predictive models of tundra ecosystem change. In summary, the capacity of *Empetrum* to cause a decoupling with soil processes (Wardle *et al.*, 2012), be unpalatable or avoided by herbivores (Danell *et al.*, 1994, Ims *et al.*, 2007, Iversen *et al.*, 2014) and be competitively superior to herbaceous plants (Mod *et al.*, 2014, Pellissier *et al.*, 2010) suggests that an increase in its abundance is likely to drive a trajectory of tundra communities and ecosystems towards slower process rates and lower biodiversity. Such change may be indicative of ecosystem retrogression (Peltzer *et al.*, 2010, Wardle *et al.*, 2004). As such our results substantiate

the importance of understanding the dynamics of niche constructor species and include them in predictive models of climate change.

Conclusion

In this study, tundra plant community changes along a temperature gradient were clearly modified by the presence of the common allelopathic dwarf shrub *Empetrum nigrum* and to a marginal degree by the large herbivore *Rangifer tarandus*. More specifically we found the increase in herbaceous plant biomass with increasing temperature to be reduced in the presence of *Empetrum*, whereas we found the biomass of woody plants to be enhanced. Importantly, we also found the biomass of *Empetrum* to increase with increasing temperature. Higher *Rangifer* density negatively affected biomass of forbs and grasses and abundance of inflorescences, and positively, although to a small extent, *Empetrum* biomass. Based on these results we argue for the inclusion of niche constructor species in predictive models of climate change due to their ecosystem-modifying role.

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References

- Aerts R (2010) Nitrogen-dependent recovery of subarctic tundra vegetation after simulation of extreme winter warming damage to *Empetrum hermaphroditum*. *Global Change Biology*, **16**, 1071-1081.
- Aerts R, Cornelissen JHC, Dorrepaal E (2006) Plant performance in a warmer world: general responses of plants from cold, northern biomes and the importance of winter and spring events. *Plant Ecology*, **182**, 65-77.
- Bell JNB, Tallis JH (1973) Biological flora of British-Isles - *Empetrum nigrum* L. *Journal of Ecology*, **61**, 289-305.
- Bernes C, Bråthen KA, Forbes BC, Speed JD, Moen J (2015) What are the impacts of reindeer/caribou (*Rangifer tarandus* L.) on arctic and alpine vegetation? A systematic review. *Environmental Evidence*, **4**, 1-26.
- Blois JL, Williams JW, Fitzpatrick MC, Jackson ST, Ferrier S (2013) Space can substitute for time in predicting climate-change effects on biodiversity. *Proceedings of the National Academy of Sciences*, **110**, 9374-9379.
- Bokhorst S, Bjerke JW, Bowles FW, Melillo J, Callaghan TV, Phoenix GK (2008) Impacts of extreme winter warming in the sub-Arctic: growing season responses of dwarf shrub heathland. *Global Change Biology*, **14**, 2603-2612.
- Bråthen KA, Fodstad CH, Gallet C (2010) Ecosystem disturbance reduces the allelopathic effects of *Empetrum hermaphroditum* humus on tundra plants. *Journal of Vegetation Science*, **21**, 786-795.
- Bråthen KA, González VT, Iversen M, Killengreen S, Ravolainen VT, Ims RA, Yoccoz NG (2007a) Endozoochory varies with ecological scale and context. *Ecography*, **30**, 308-320.
- Bråthen KA, Hagberg O (2004) More efficient estimation of plant biomass. *Journal of Vegetation Science*, **15**, 653-660.
- Bråthen KA, Ims RA, Yoccoz NG, Fauchald P, Tveraa T, Hausner VH (2007b) Induced shift in ecosystem productivity ? Extensive scale effects of abundant large herbivores. *Ecosystems*, **10**, 773-789.

- Bråthen KA, Lortie C (2016) A portfolio effect of shrub canopy height on species richness in both stressful and competitive environments. *Functional Ecology*, **30**, 60-69.
- Bråthen KA, Ravolainen V (2015) Niche construction by growth forms is as strong a predictor of species diversity as environmental gradients. *Journal of Ecology*, **103**, 701-713.
- Buizer B, Weijers S, Van Bodegom PM *et al.* (2012) Range shifts and global warming: ecological responses of *Empetrum nigrum* L. to experimental warming at its northern (high Arctic) and southern (Atlantic) geographical range margin. *Environmental Research Letters*, **7**, 025501.
- Buntgen U, Hellmann L, Tegel W *et al.* (2015) Temperature-induced recruitment pulses of Arctic dwarf shrub communities. *Journal of Ecology*, **103**, 489-501.
- Büntgen U, Hellmann L, Tegel W *et al.* (2015) Temperature-induced recruitment pulses of Arctic dwarf shrub communities. *Journal of Ecology*, **103**, 489-501.
- Chapin FS, Bretharte MS, Hobbie SE, Zhong HL (1996) Plant functional types as predictors of transient responses of arctic vegetation to global change. *Journal of Vegetation Science*, **7**, 347-358.
- Chapin FS, Sturm M, Serreze MC *et al.* (2005) Role of land-surface changes in Arctic summer warming. *Science*, **310**, 657-660.
- Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024-1026.
- Christie KS, Bryant JP, Gough L, Ravolainen VT, Ruess RW, Tape KD (2015) The Role of Vertebrate Herbivores in Regulating Shrub Expansion in the Arctic: A Synthesis. *Bioscience*, **65**, 1123-1133.
- Collantes MB, Anchorena J, Cingolani AM (1999) The steppes of Tierra del Fuego: floristic and growthform patterns controlled by soil fertility and moisture. *Plant Ecology*, **140**, 61-75.
- Cornelissen JHC, Quested HM, Gwynn-Jones D *et al.* (2004) Leaf digestibility and litter decomposability are related in a wide range of subarctic plant species and types. *Functional Ecology*, **18**, 779-786.

- Cornelissen JHC, Van Bodegom PM, Aerts R *et al.* (2007) Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecology Letters*, **10**, 619-627.
- Danell K, Utsi PM, Palo RT, Eriksson O (1994) Food plant selection by reindeer during winter in relation to plant quality. *Ecography*, **17**, 153-158.
- Daubenmire R (1968) *Plant communities. A textbook of plant synecology*, New York, Harper & Row.
- De Long JR, Dorrepaal E, Kardol P, Nilsson M-C, Teuber LM, Wardle DA (2016) Understory plant functional groups and litter species identity are stronger drivers of litter decomposition than warming along a boreal forest post-fire successional gradient. *Soil Biology and Biochemistry*, **98**, 159-170.
- Den Herder M, Virtanen R, Roininen H (2008) Reindeer herbivory reduces willow growth and grouse forage in a forest-tundra ecotone. *Basic and Applied Ecology*, **9**, 324-331.
- Elmendorf SC, Henry GHR, Hollister RD *et al.* (2012a) Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters*, **15**, 164-175.
- Elmendorf SC, Henry GHR, Hollister RD *et al.* (2012b) Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change*, **2**, 453-457.
- Elmendorf SC, Henry GHR, Hollister RD *et al.* (2015) Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns. *Proceedings of the National Academy of Sciences*, **112**, 448-452.
- Epstein HE, Reynolds MK, Walker DA, Bhatt US, Tucker CJ, Pinzon JE (2012) Dynamics of aboveground phytomass of the circumpolar Arctic tundra during the past three decades. *Environmental Research Letters*, **7**, 015506.
- Felde VA, Kapfer J, Grytnes J-A (2012) Upward shift in elevational plant species ranges in Sikkildalen, central Norway. *Ecography*, **35**, 922-932.

- Francini G, Liiri M, Männistö M, Stark S, Kytöviita M-M (2014) Response to reindeer grazing removal depends on soil characteristics in low Arctic meadows. *Applied Soil Ecology*, **76**, 14-25.
- Gallet C, Nilsson MC, Zackrisson O (1999) Phenolic metabolites of ecological significance in *Empetrum hermaphroditum* leaves and associated humus. *Plant and Soil*, **210**, 1-9.
- González VT, Bråthen KA, Ravolainen VT, Iversen M, Hagen SB (2010) Large-scale grazing history effects on Arctic-alpine germinable seed banks. *Plant Ecology*, **207**, 321-331.
- González VT, Junttila O, Lindgård B, Reiersen R, Trost K, Bråthen KA (2015) Batatasin-III and the allelopathic capacity of *Empetrum nigrum*. *Nordic Journal of Botany*, **33**, 225-231.
- Gottfried M, Pauli H, Futschik A *et al.* (2012) Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, **2**, 111-115.
- Graae BJ, Ejrnæs R, Lang SI, Meineri E, Ibarra PT, Bruun HH (2011) Strong microsite control of seedling recruitment in tundra. *Oecologia*, **166**, 565-576.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *International journal of climatology*, **25**, 1965-1978.
- Hobbie SE (1992) Effects of plant species on nutrient cycling. *Trends in Ecology & Evolution*, **7**, 336-339.
- Huntington H (2013) Provisioning and cultural services. In: *Arctic biodiversity assesment. Status and trends in Arctic biodiversity*. (ed Meltofte H) pp Page. Akureyri, Conservation of Arctic Flora and Fauna.
- Ims RA, Ehrich D, Forbes BC *et al.* (2013) Terrestrial Ecosystems. In: *Arctic Biodiversity Assessment. Status and trends in Arctic biodiversity*. . (ed Meltofte H) pp Page. Akureyri, Iceland, Conservation of Arctic Flora and Fauna.
- Ims RA, Henden J-A, Killengreen ST (2008) Collapsing population cycles. *Trends in Ecology & Evolution*, **23**, 79-86.
- Ims RA, Yoccoz NG, Bråthen KA, Fauchald P, Tveraa T, Hausner V (2007) Can reindeer overabundance cause a trophic cascade? *Ecosystems*, **10**, 607-622.

- Iversen M, Fauchald P, Langeland K, Ims RA, Yoccoz NG, Bråthen KA (2014) Phenology and cover of plant growth forms predict herbivore habitat selection in a high latitude ecosystem. *Plos One*, **9(6)**: e100780.
- Johansen B, Tømmervik H, Karlsen SR (1995) Vegetasjons- og beitekartlegging i Finnmark og Nord-Troms. pp Page, Tromsø, Norway, NORUT Informasjonsteknologi AS.
- Kaarlejärvi E, Baxter R, Hofgaard A *et al.* (2012) Effects of warming on shrub abundance and chemistry drive ecosystem-level changes in a forest–tundra ecotone. *Ecosystems*, **15**, 1219-1233.
- Kaarlejärvi E, Eskelinen A, Olofsson J (2013) Herbivory prevents positive responses of lowland plants to warmer and more fertile conditions at high altitudes. *Functional Ecology*, **27**, 1244-1253.
- Klanderud K, Birks HJB (2003) Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *The Holocene*, **13**, 1-6.
- Klein JA, Harte J, Zhao XQ (2004) Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. *Ecology Letters*, **7**, 1170-1179.
- Körner C (2003) *Alpine plant life: functional plant ecology of high mountain ecosystems*, Berlin, Springer.
- Kullman L (2010) A richer, greener and smaller alpine world: review and projection of warming-induced plant cover change in the Swedish Scandes. *Ambio*, **39**, 159-169.
- Larsen KS, Michelsen A, Jonasson S, Beier C, Grogan P (2012) Nitrogen uptake during fall, winter and spring differs among plant functional groups in a subarctic heath ecosystem. *Ecosystems*, **15**, 927-939.
- Le Roux PC, Pellissier L, Wisz MS, Luoto M (2014) Incorporating dominant species as proxies for biotic interactions strengthens plant community models. *Journal of Ecology*, **102**, 767-775.
- Lenoir J, Gégout JC, Marquet PA, De Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, **320**, 1768-1771.

- Matthews B, De Meester L, Jones CG *et al.* (2014) Under niche construction: an operational bridge between ecology, evolution, and ecosystem science. *Ecological Monographs*, **84**, 245-263.
- Michelsen A, Schmidt I, Jonasson S, Quarmby C, Sleep D (1996) Leaf ¹⁵N abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non-and arbuscular mycorrhizal species access different sources of soil nitrogen. *Oecologia*, **105**, 53-63.
- Mod HK, Heikkinen RK, Le Roux PC, Wisz MS, Luoto M (2016) Impact of biotic interactions on biodiversity varies across a landscape. *Journal of Biogeography*, n/a-n/a.
- Mod HK, Le Roux PC, Luoto M (2014) Outcomes of biotic interactions are dependent on multiple environmental variables. *Journal of Vegetation Science*, **25**, 1024-1032.
- Moen J, Danell Ö (2003) Reindeer in the Swedish mountains: An assessment of grazing impacts. *Ambio*, **32**, 397-402.
- Moore ID, Grayson RB, Landson AR (1991) Digital terrain modelling: A review of hydrological, geomorphological, and biological applications. *Hydrological Processes*, **5**, 3-30.
- Mörsdorf MA, Ravolainen VT, Støvern LE, Yoccoz NG, Jónsdóttir IS, Bråthen KA (2015) Definition of sampling units begets conclusions in ecology: the case of habitats for plant communities. *PeerJ*, **3**, e815.
- Myers-Smith IH, Elmendorf SC, Beck PSA *et al.* (2015) Climate sensitivity of shrub growth across the tundra biome. *Nature Clim. Change*, **5**, 887-891.
- Myers-Smith IH, Forbes BC, Wilmking M *et al.* (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters*, **6**.
- Nilsson MC, Hogberg P, Zackrisson O, Wang FY (1993) Allelopathic effects by *Empetrum hermaphroditum* on development and nitrogen uptake by roots and mycorrhizae of *Pinus sylvestris*. *Canadian Journal of Botany*, **71**, 620-628.
- Nilsson MC, Wardle DA (2005) Understorey vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. *Frontiers in Ecology and the Environment*, **3**, 421-428.

- Nilsson MC, Zackrisson O (1992) Inhibition of Scots pine seedling establishment by *Empetrum hermaphroditum*. *Journal of Chemical Ecology*, **18**, 1857-1870.
- Oberski D (2014) lavaan.survey: an R package for complex survey analysis of structural equation models. *J. Stat. Softw.*, **57**, 1-27.
- Odling-Smee J, Erwin DH, Palkovacs EP, Feldman MW, Laland KN (2013) Niche construction theory: A practical guide for ecologists. *Quarterly Review of Biology*, **88**, 3-28.
- Olofsson J, Ericson L, Torp M, Stark S, Baxter R (2011) Carbon balance of Arctic tundra under increased snow cover mediated by a plant pathogen. *Nature Climate Change*, **1**, 220-223.
- Olofsson J, Kitti H, Rautiainen P, Stark S, Oksanen L (2001) Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. *Ecography*, **24**, 13-24.
- Olofsson J, Oksanen L, Callaghan T, Hulme PE, Oksanen T, Suominen O (2009) Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology*, **15**, 2681-2693.
- Olofsson J, Tømmervik H, Callaghan TV (2012) Vole and lemming activity observed from space. *Nature Climate Change*, **2**, 880-883.
- Pajunen AM, Oksanen J, Virtanen R (2011) Impact of shrub canopies on understorey vegetation in western Eurasian tundra. *Journal of Vegetation Science*, **22**, 837-846.
- Pellissier L, Bråthen KA, Pottier J *et al.* (2010) Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. *Ecography*, **33**, 1004-1014.
- Pellissier L, Bråthen KA, Vittoz P *et al.* (2013) Thermal niches are more conserved at cold than warm limits in arctic-alpine plant species. *Global Ecology and Biogeography*, **22**, 933-941.
- Peltzer DA, Wardle DA, Allison VJ *et al.* (2010) Understanding ecosystem retrogression. *Ecological Monographs*, **80**, 509-529.
- Pinheiro JC, Bates DM (2000) *Linear mixed-effects models: basic concepts and examples*, New York, Springer.

- Popp M, Mirré V, Brochmann C (2011) A single Mid-Pleistocene long-distance dispersal by a bird can explain the extreme bipolar disjunction in crowberries (*Empetrum*). *Proceedings of the National Academy of Sciences*, **108**, 6520-6525.
- Post E (2013) Erosion of community diversity and stability by herbivore removal under warming. *Proceedings of the Royal Society of London B: Biological Sciences*, **280**, 2012-2722.
- Preece C, Callaghan TV, Phoenix GK (2012) Impacts of winter icing events on the growth, phenology and physiology of sub-arctic dwarf shrubs. *Physiologia Plantarum*, **146**, 460-472.
- Preece C, Phoenix GK (2014) Impact of early and late winter icing events on sub-arctic dwarf shrubs. *Plant Biology*, **16**, 125-132.
- Ravolainen VT, Bråthen KA, Yoccoz NG, Nguyen JK, Ims RA (2014) Complementary impacts of small rodents and semi-domesticated ungulates limit tall shrub expansion in the tundra. *Journal of Applied Ecology*, **51**, 234-241.
- Ravolainen VT, Yoccoz NG, Bråthen KA, Ims RA, Iversen M, González VT (2010) Additive partitioning of diversity reveals no scale-dependent impacts of large ungulates on the structure of tundra plant communities. *Ecosystems*, **13**, 157-170.
- Rosseel Y, Oberski D, Byrnes J, Vanbrabant L, Savalei V (2013) lavaan: latent variable analysis. pp Page, R Foundation for Statistical Computing.
- Rustad L, Campbell J, Marion G *et al.* (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, **126**, 543-562.
- Soininen EM, Ravolainen VT, Bråthen KA, Yoccoz NG, Gielly L, Ims RA (2013a) Arctic small rodents have diverse diets and flexible food selection. *Plos One*, **8**, e68128.
- Soininen EM, Zinger L, Gielly L *et al.* (2013b) Shedding new light on the diet of Norwegian lemmings: DNA metabarcoding of stomach content. *Polar Biology*, **36**, 1069-1076.
- Sorensen PL, Clemmensen KE, Michelsen A, Jonasson S, Ström L (2008) Plant and microbial uptake and allocation of organic and inorganic nitrogen related to plant

- growth forms and soil conditions at two subarctic tundra sites in Sweden. *Arctic, Antarctic, and Alpine Research*, **40**, 171-180.
- Tarbuck EJ, Lutgens FK (1992) *The earth. An introduction to physical geology*, New York, Macmillan Publishing Company.
- Tveraa T, Fauchald P, Gilles Yoccoz N, Anker Ims R, Aanes R, Arild Høgda K (2007) What regulate and limit reindeer populations in Norway? *Oikos*, **116**, 706-715.
- Tyrbirk K, Nilsson MC, Michelson A *et al.* (2000) Nordic *Empetrum* dominated ecosystems: Function and susceptibility to environmental changes. *Ambio*, **29**, 90-97.
- Väisänen M, Martz F, Kaarlejärvi E, Julkunen-Tiitto R, Stark S (2013) Phenolic responses of mountain crowberry (*Empetrum nigrum* ssp. *hermaphroditum*) to global climate change are compound specific and depend on grazing by reindeer (*Rangifer tarandus*). *Journal of Chemical Ecology*, **39**, 1390-1399.
- Väisänen M, Ylanne H, Kaarlejärvi E, Sjögersten S, Olofsson J, Crout N, Stark S (2014) Consequences of warming on tundra carbon balance determined by reindeer grazing history. *Nature Climate Change*, **4**, 384-388.
- Virtanen R, Luoto M, Rämä T, Mikkola K, Hjort J, Grytnes JA, Birks HJB (2010) Recent vegetation changes at the high-latitude tree line ecotone are controlled by geomorphological disturbance, productivity and diversity. *Global Ecology and Biogeography*, **19**, 810-821.
- Wada N, Shimono M, Miyamoto M, Kojima S (2002) Warming effects on shoot developmental growth and biomass production in sympatric evergreen alpine dwarf shrubs *Empetrum nigrum* and *Loiseleuria procumbens*. *Ecological Research*, **17**, 125-132.
- Walker DA, Raynolds MK, Daniels FJA *et al.* (2005) The Circumpolar Arctic vegetation map. *Journal of Vegetation Science*, **16**, 267-282.
- Wallstedt A, Gallet C, Nilsson MC (2005) Behaviour and recovery of the secondary metabolite batatasin-III from boreal forest humus: influence of temperature, humus type and microbial community. *Biochemical Systematics and Ecology*, **33**, 385-407.

- Wallstedt A, Sommarin M, Nilsson MC, Munson AD, Margolis HA (2001) The inhibition of ammonium uptake in excised birch (*Betula pendula*) roots by batatasin-III. *Physiologia Plantarum*, **113**, 368-376.
- Wardle DA, Gundale MJ, Jäderlund A, Nilsson M-C (2012) Decoupled long-term effects of nutrient enrichment on aboveground and belowground properties in subalpine tundra. *Ecology*, **94**, 904-919.
- Wardle DA, Jonsson M (2013) Long-term resilience of above- and belowground ecosystem components among contrasting ecosystems. *Ecology*, **95**, 1836-1849.
- Wardle DA, Nilsson MC, Gallet C, Zackrisson O (1998) An ecosystem-level perspective of allelopathy. *Biological Reviews of the Cambridge Philosophical Society*, **73**, 305-319.
- Wardle DA, Walker LR, Bardgett RD (2004) Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science*, **305**, 509-513.
- Wilson PJ, Thompson K, Hodgson JG (1999) Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist*, **143**, 155-162.
- Wilson SD, Nilsson C (2009) Arctic alpine vegetation change over 20 years. *Global Change Biology*, **15**, 1676-1684.
- Wipf S (2010) Phenology, growth, and fecundity of eight subarctic tundra species in response to snowmelt manipulations. *Plant Ecology*, **207**, 53-66.
- Wipf S, Rixen C, Mulder CPH (2006) Advanced snowmelt causes shift towards positive neighbour interactions in a subarctic tundra community. *Global Change Biology*, **12**, 1496-1506.
- Wookey PA, Aerts R, Bardgett RD *et al.* (2009) Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. *Global Change Biology*, **15**, 1153-1172.
- Ylänne H, Stark S, Tolvanen A (2015) Vegetation shift from deciduous to evergreen dwarf shrubs in response to selective herbivory offsets carbon losses: evidence from 19 years of warming and simulated herbivory in the subarctic tundra. *Global Change Biology*, **21**, 3696-3711.

Zamin TJ, Grogan P (2013) Caribou exclusion during a population low increases deciduous and evergreen shrub species biomass and nitrogen pools in low Arctic tundra. *Journal of Ecology*, **101**, 671-683.

Figure Legends

Figure 1. Summer temperatures across northern Fennoscandia including landscape areas where plant communities were analyzed (upper panel) and an overview of the study design applied in each landscape area (lower panel). In the upper panel the borders represent the 20 *Rangifer* husbandry districts and the red squares represent the landscape areas. In the lower panel the nested design for each landscape area, geographically positioned a priori to the field season, is shown. Within each landscape area a random set of maximum 21 squares of 200 m x 200 m were analyzed by running a transect from the square center in a random direction. Plots were regularly placed along each transect representing a plant community and each plot was analyzed by the point intercept method using three pins.

Figure 2. Structural equation model representing connections between *Empetrum*, temperature, *Rangifer* and herbaceous and woody growth forms supported by the data. Blue text represents positive effects, red text represents negative effects. Black arrows indicate significant effects, grey arrows indicate effects no longer significant under the adjustment of the model when accounting for the hierarchical study design. Only the interaction term significant in both models is presented: the interaction between *Empetrum* and temperature on herbaceous biomass. Model test statistic = 4.825, with 2 model degrees of freedom and $p = 0.090$ (indicating close model-data fit). The robust test statistic = 1.138 (model also considering the hierarchical design), with 2 model degrees of freedom and $p = 0.566$ (again indicating close model-data fit). Comparative Fit Index = 0.996 and Root Mean Square Error of Approximation = 0.031, further indicate close model fit.

Figure 3. The effect of increasing temperature (warmest quarter) and *Rangifer tarandus* density (high vs. low) on the predicted values of aboveground biomass (g m^{-2}) and the abundance of berries (point intercept frequency) of *Empetrum nigrum* presented on a $\log_e(x+1)$ scale. The linear regressions are based on predicted values from a lme model output

and are presented with $\pm 95\%$ confidence bands.

Figure 4. The effect of increasing temperature (warmest quarter) and *Rangifer tarandus* density (high vs. low) and increasing levels of *Empetrum* biomass on the predicted values of **a)** the aboveground biomass (g m^{-2}) of herbaceous (forbs, grasses and sedges), woody (deciduous and evergreen shrubs) growth forms and on **b)** the abundance of species richness and inflorescences (point intercept frequency) in the plant communities. The three panels represent communities with 0%, 25% (20-30%) and 75% (70-80%) of community biomass occupied by *Empetrum* biomass. All variables are presented on a $\log_e (x+1)$ scale. The linear regressions are based on predicted values from a lme model output and are presented with $\pm 95\%$ confidence bands.

Figure 1.

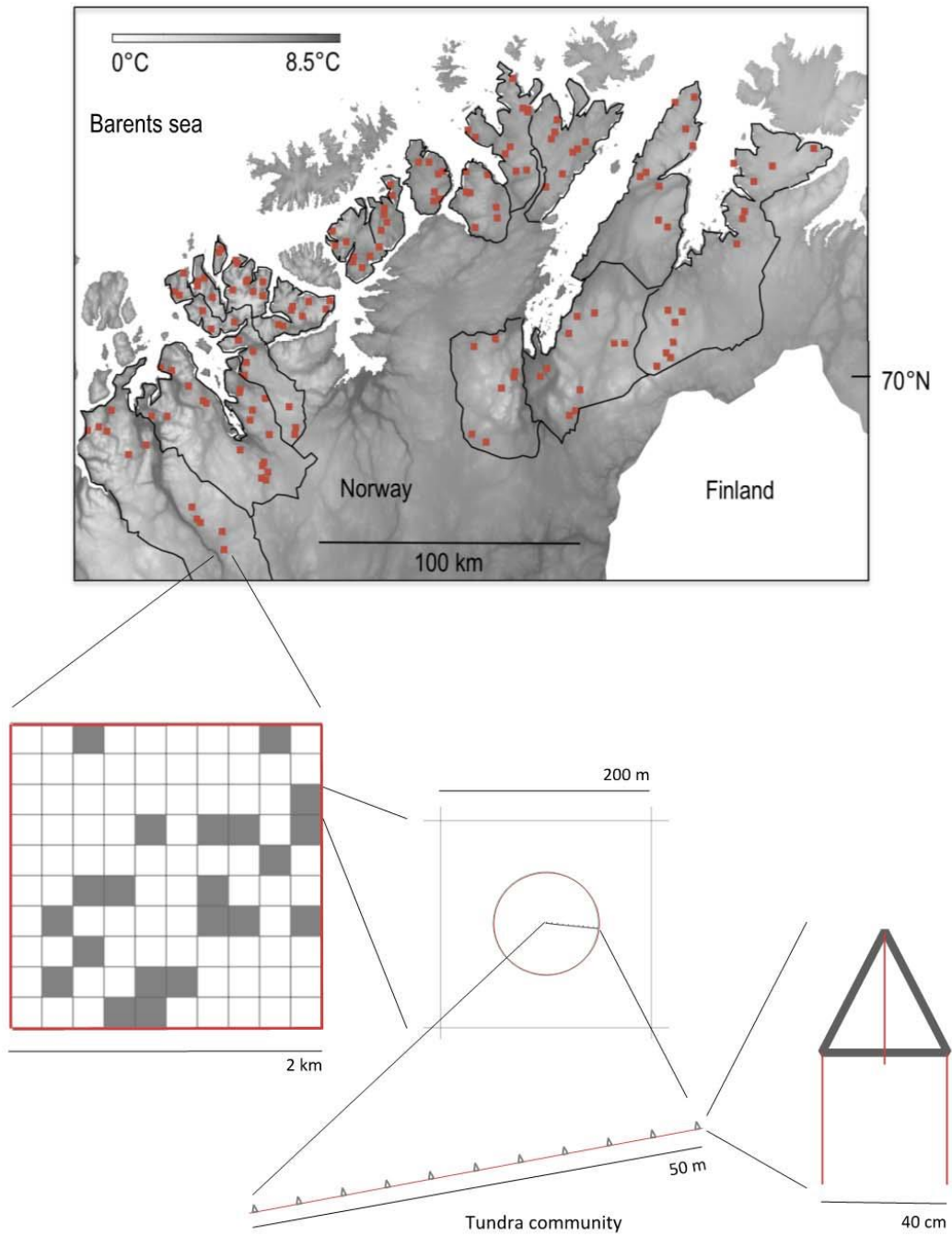
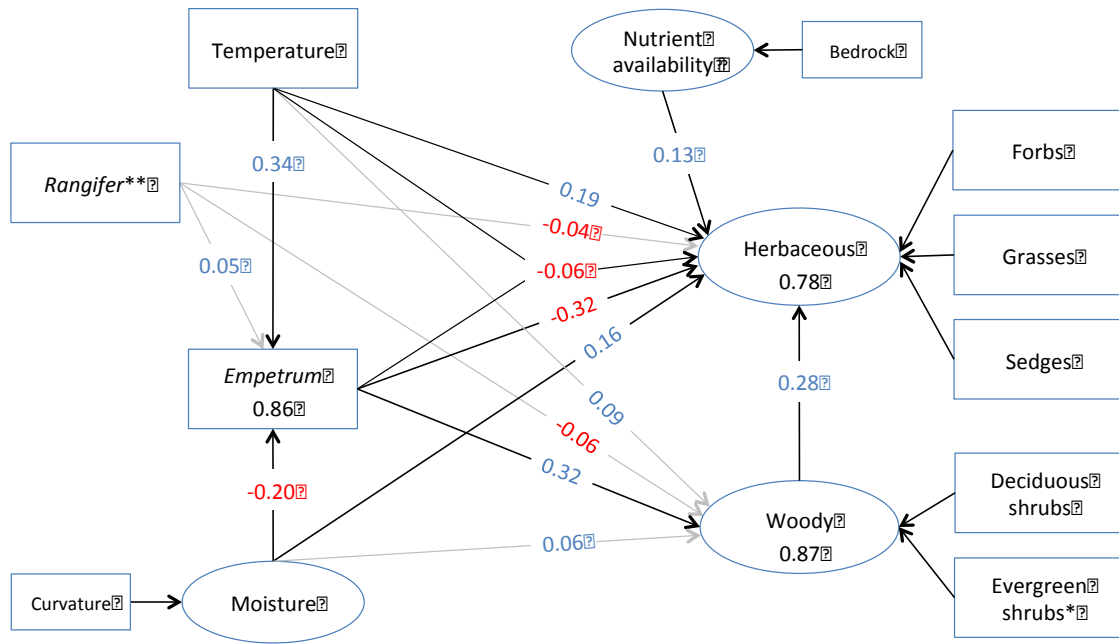


Figure 2



*excluding **Empetrum**

**anthropogenically determined

Figure 3.

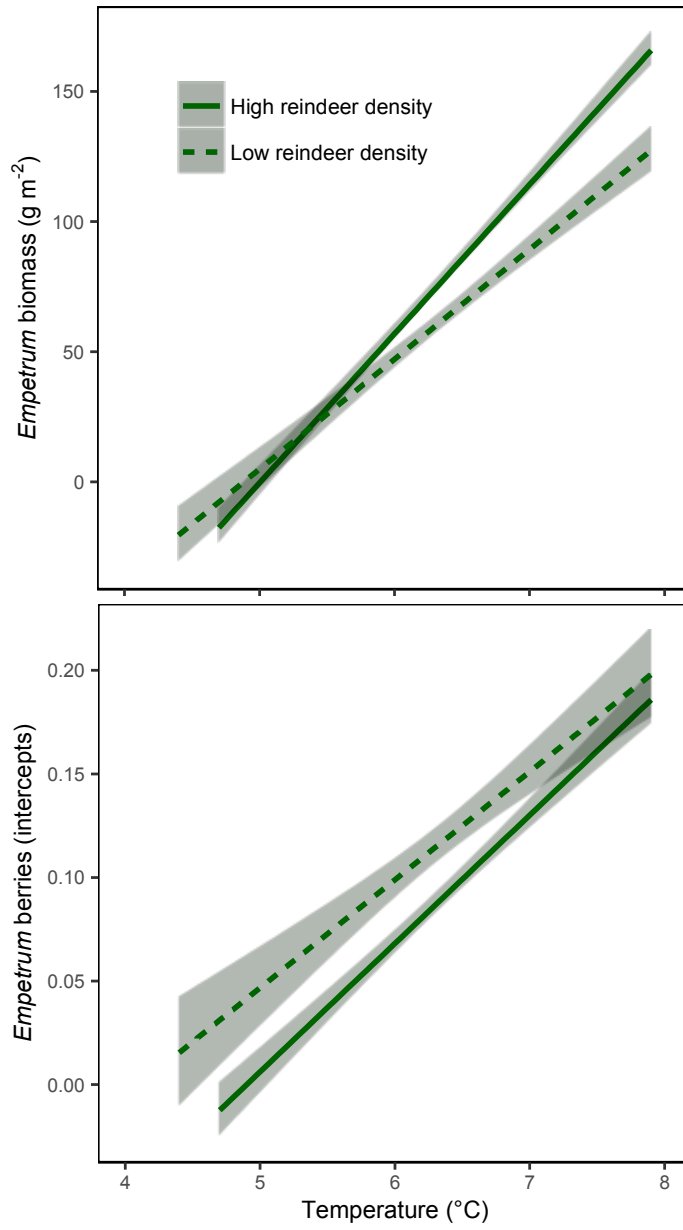


Figure 4a

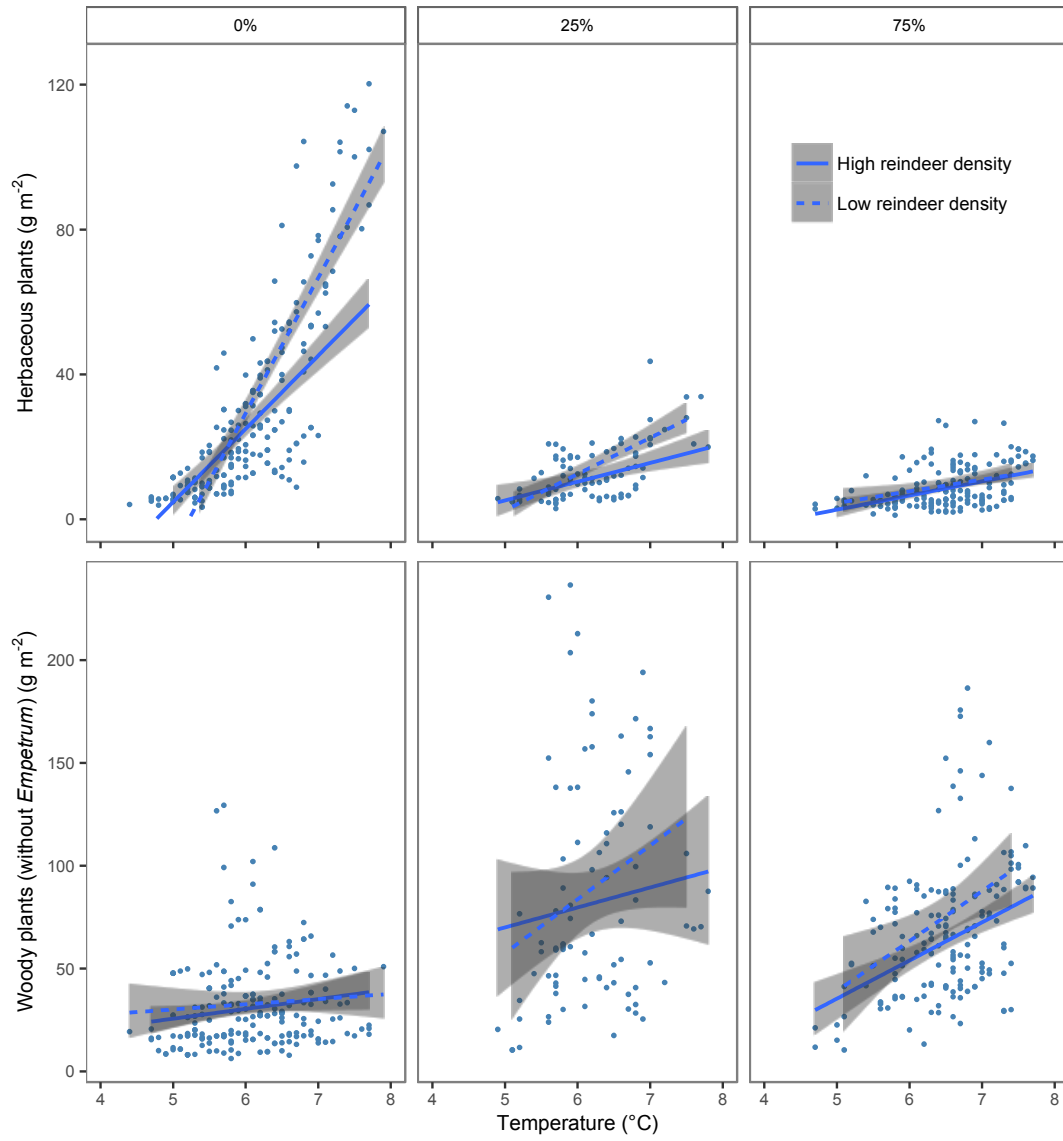


Figure 4b

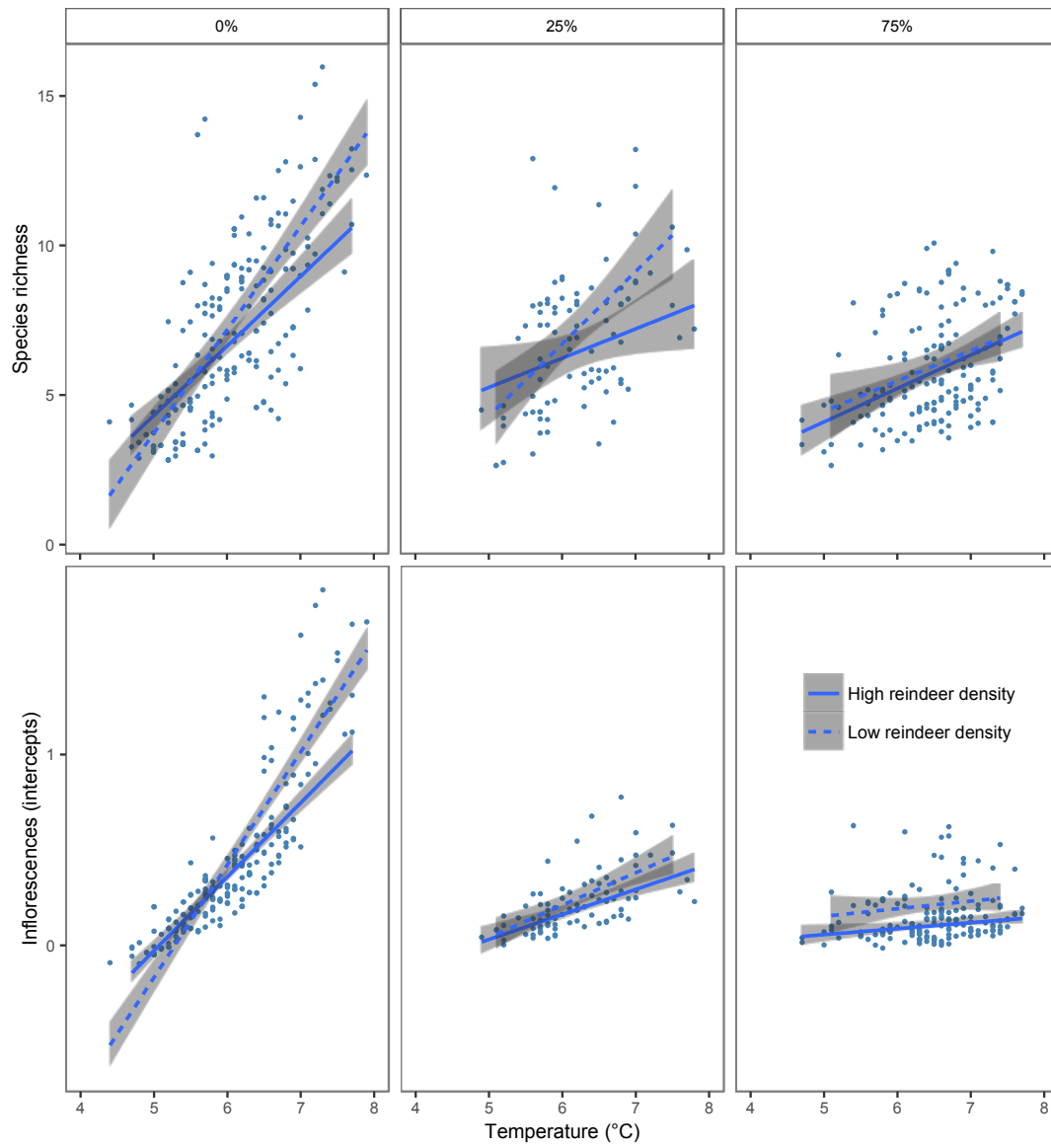


Table 1. Total and average species pool and aboveground biomass presented per growth form and for *Empetrum nigrum* and in total across the tundra plant communities included in this study.

Growth form	Species pool per growth form	Average species pool or presence** (mean \pm SD)	Aboveground biomass (mean g m ⁻² \pm SD)
Forbs	105	1.18 \pm 1.84	5.4 \pm 11.6
Grasses	23	1.34 \pm 1.47	9.1 \pm 17
Sedges	47	1.31 \pm 1.37	7.8 \pm 14.8
Deciduous shrubs	17	2.14 \pm 1.14	63.5 \pm 58.3
Evergreen shrubs*	9	1.02 \pm 0.93	24 \pm 32.4
Vascular cryptogams	21	0.16 \pm 0.44	0.9 \pm 4.0
<i>Empetrum nigrum</i> **		0.85 \pm 0.35	118 \pm 106.6
Total per plant community		8.08 \pm 4.34	228.7 \pm 146.6

*Not including *Empetrum*

Table 2. Standardized coefficients (\pm 95% C.I.) of fixed effects predictors extracted from mixed effects models on community and *Empetrum* characteristics, along with their random factors (SD \pm 95% C.I.). All models include temperature (warmest quarter), *Empetrum* biomass and *Rangifer* density (high or low) as predictors along with their significant interactions. The evergreen shrub biomass is not including *Empetrum* biomass, and the inflorescences are not including *Empetrum* inflorescences. Statistically significant predictors have confidence intervals that do not overlap with zero, and non-significant predictors are presented in grey. Growth form names are short for their biomasses, whereas berries and inflorescences are short for their point intercepts.

Predictors, fixed variables				Random factors		
Temperature	<i>Empetrum</i> biomass	<i>Rangifer</i> density	Temp x <i>Empetrum</i> bm	District pairs	Landscape areas	
Response variables						
<i>Empetrum</i>						
<i>nigrum</i>						
Biomass	0.642 (0.492, 0.792) -	0.316 (0.005, 0.627) -		0.308 (0.123, 0.792 (0.658, 0.771)	0.954)	

Berries	0.016 0.140)	(-0.003, 0.066 (0.052, 0.081)	-0.032 0.0001)	(-0.064, - 0.023 (0.010, 0.036)	0.043 0.081)	(0.023, 0.052 0.077)	(0.035,
<i>Community characteristics</i>							
Species richness	0.204 (0.159, 0.250)	-0.035 0.010)	(-0.060, - -0.057 (-0.150, 0.035)	0.213 0.362)	(0.126, 0.245 0.288)	(0.208,	
Inflorescences	0.083 (0.050, 0.117)	-0.079 0.056)	(-0.101, - -0.080 (-0.142, -0.018)	-0.052 0.030)	(-0.073, - 0.066 0.139)	(0.031, 0.139 0.175)	(0.109,
Herbaceous plants	0.446 (0.340, 0.553)	-0.343 0.278)	(-0.407, - -0.137 (-0.346, 0.072)	-0.077 0.017)	(-0.137, - 0.307 0.562)	(0.168, 0.527 0.628)	(0.443,
Woody plants	0.281 (0.188, 0.375)	0.299 (0.246, 0.352)	-0.038 (-0.226, 0.150)	0.065 (0.016, 0.114)	0.450 0.765)	(0.265, 0.496 0.583)	(0.422,
<i>Growth forms</i>							
Forbs	0.325 (0.221, 0.428)	-0.236 0.177)	(-0.295, - -0.280 (-0.488, -0.072)	0.403 0.693)	(0.234, 0.545 0.646)	(0.460,	
Grasses	0.471 (0.363, 0.579)	-0.136 0.071)	(-0.201, - -0.265 (-0.469, -0.062)	0.210 0.462)	(0.096, 0.504 0.607)	(0.419,	

Sedges	0.183 (0.082, 0.283)	-0.289 (-0.352, -0.226)	-0.165 (-0.032, 0.363)	0.399 (0.233, 0.488)	0.681 (0.406, 0.587)
Deciduous shrubs	0.320 (0.216, 0.425)	0.200 (0.141, 0.259)	-0.025 (-0.233, 0.184)	0.451 (0.260, 0.545)	0.785 (0.464, 0.641)
Evergreen shrubs	0.192 (0.063, 0.322)	0.596 (0.515, 0.676)	0.006 (-0.222, 0.234)	0.617 (0.369, 0.527)	1.030 (0.425, 0.653)
