Effects of Warming on Shrub Abundance and Chemistry Drive Ecosystem-Level Changes in a Forest–Tundra Ecotone

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Abstract:

Tundra vegetation is responding rapidly to on-going climate warming. The changes in plant abundance and chemistry might have cascading effects on tundra food webs, but an integrated understanding of how the responses vary between habitats and across environmental gradients is lacking. We assessed responses in plant abundance and plant chemistry to warmer climate, both at species and community levels, in two different habitats. We used a long-term and multisite warming (OTC) experiment in the Scandinavian forest–tundra ecotone to investigate (i) changes in plant community composition and (ii) responses in foliar nitrogen, phosphorus, and carbon-based secondary compound concentrations in two dominant evergreen dwarf-shrubs (*Empetrum hermaphroditum* and *Vaccinium vitis-idaea*) and two deciduous shrubs (*Vaccinium myrtillus* and *Betula nana*). We found that initial plant community composition, and the functional traits of these plants, will determine the responsiveness of the community composition, and thus community traits, to experimental warming. Although changes in plant chemistry within species were minor, alterations in plant community composition drive changes in community-level nutrient concentrations. In view of projected climate change, our results suggest that plant abundance will increase in the future, but nutrient concentrations in the tundra field layer vegetation will decrease. These effects are large enough to have knock-on consequences for major ecosystem processes like herbivory and nutrient cycling. The reduced food quality could lead to weaker trophic cascades and weaker top down control of plant com- munity biomass and composition in the future. However, the opposite effects in forest indicate that these changes might be obscured by advancing tree- line forests.

Keywords:

Introduction:

Arctic-alpine vegetation is currently changing to- ward a more thermophilic state (Gottfried and others 2012). Trees are expanding into tundra (Tømmervik and others 2009; Harsch and others 2009), and tundra is becoming greener (Walker and others 2009; Bhatt and others 2010). These

changes are assumed to be driven by warmer temperatures (Harsch and others 2009; Bhatt and others 2010) although social factors, such as industrial development or nomadic reindeer herding, can also be important (Walker and others 2009; Forbes and others 2009). Moreover, studies on treeline ecotone dynamics throughout Scandinavia reveal diverse regional patterns due to local climate, herbivory, and land-use history (Dalen and Hofgaard 2005; Van Bogaert and others 2011). Meta-analyses of warming experiments on tundra (Dormann and Woodin 2002; Walker and others 2006; Elmendorf and others 2012) and dendrochronological studies (Forbes and others 2010; Blok and others 2011) indicate that increased greenness is strongly related to increased plant abundance in response to warming. Indeed, a number of observational studies have documented a rapid circumpolar increase of deciduous shrubs, especially willows (Tape and others 2006; Myers-Smith and others 2011) and dwarf birch (Olofsson and others 2009), which seems to drive this greening. Nevertheless, the meta-analyses paint a diverse picture of warming impacts on the other functional plant groups; for example, only Walker and others (2006) recorded an increase of graminoids, whereas the two other meta-analyses reported no net effect on graminoids, because of diverse species-level responses within the group (Dormann and Woodin 2002; Elmendorf and others 2012). Because all functional groups, and the species within them, have different morphological and chemical traits, these changes in species composition can also drive changes in community traits (Graglia and others 2001; Hansen and others 2005; Sundqvist and others 2011). Accelerated growth and altered environmental conditions may also transform plant chemistry within species. A global meta-analysis (Reich and Oleksyn 2004) revealed that plant leaves tend to have lower nutrient concentrations in warmer temperatures, which corresponds with the findings from altitudinal gradients, where plants from lower altitudes have lower nitrogen (N) (Körner and others 1986) and phosphorus (P) (Kitayama and Aiba 2002) concentrations than plants from higher altitudes. Furthermore, according to the plant defence hypothesis (Coley and others 1985), benign, less-stressful, environmental conditions should diminish plant allocation to carbon-based secondary compounds (CBSC).However, after more than 20 years of research and debate, solid empirical support for this hypothesis is still lacking, and a mechanism for the suggested allocation transformation is unclear. In the Arctic, especially, studies on the links between warming and CBSCs are limited in number and also local in scope, which further con- strains the detection of large-scale patterns (see however (Graglia and others 2001). Changes in chemical properties of the plant com- munity, driven by changes in species composition or changes in chemistry within species, may also influence food web interactions (Schmitz 2008) and nutrient cycling (Cornelissen and others 2007). Plants, in general, have higher carbon(C) to N and C to P ratios compared to the elemental composition of herbivores and decomposers, which in turn have consistently high levels of N and P relative to C (Sterner and Elser 2002). This stoichiometrical mismatch may weaken the importance of herbivores in regulating plant biomass, leading to reduced digestibility of the vegetation (Sterner and Elser 2002) and the slower rate of plant litter decomposition (Cornelissen and others 2007). The concentrations of CBSCs, such as carbon-based tannins and phenolics, may further reduce the digestibility of plants to herbivores (Bryant and Kuropat 1980; Iason 2005; Dearingandothers2005) and the decomposability of their litter in the soil (Cornelissen and others 2004). The effects of a changing climate on plant abundance and chemistry are thus expected to have cascading effects on above- and belowground food webs (Schmitz 2008) with cascading effects on the function of the whole ecosystems. Based on the reasoning above, a warmer climate should accelerate the growth of plants in general, but change the composition by favouring the fastest growing species (deciduous shrubs and graminoids). Because fast growing species are expected to have high nutrient concentrations and low levels of secondary com- pounds (Coley and others 1985), both the quality and quantity of food for herbivores and litter for decomposers are expected to increase with a warmer climate. However, because changes in plant community composition and plant chemistry

have rarely been investigated simultaneously, and the response of plant chemistry to warming is known to vary be- tween sites and species (Graglia and others 2001; Hansen and others 2005), the generality of these predictions is unknown. In this study, we used a long-term and multi- site experiment to study the responses of plant abundance and plant chemistry to experimental warming. Based on the studies mentioned above, we hypothesized that warming will result in (i) accelerated growth and increased shrub abundance, especially of deciduous shrubs, (ii) increased N and P concentrations in plants, and (iii) diminished concentrations of CBSC.

Materials and Methods:

Study Species

We selected two deciduous and two evergreen dwarf-shrubs, which are common in oligotrophic arctic tundra heaths and subalpine forest understorey, as study species (note: at our study sites, graminaceous plants were present at abundances too low to be included in this analysis). These four species represent, on average, 80% of the total field layer biomass in the habitats studied (Dovrefjell = 69%, Abisko = 74%, Joatka = 95%), and can thus be used as a valid measure of field layer plant community in the oligotrophic forest–tundra eco- tone in Fennoscandia. Evergreen northern crow- berry (*Empetrum hermaphroditum* Lange ex Hagerup) and cowberry (*Vaccinium vitis-idaea* L.) are unpreferred species that mammalian herbivores feed on only occasionally (Batzli and Lesieutre 1991; Warenberg and others 1997). Our focal deciduous species, dwarf-birch (*Betula nana* L.) and bilberry (*Vaccinium myrtillus* L.), are favored by reindeer in summer (Warenberg and others 1997; Kumpula and others 2004), whereas microtine rodents feed extensively on *V. myrtillus* in winter (Kalela 1957), also as mountain hares occasionally do (Hjältén and others 2004). Hereafter, for simplicity, we refer to our four study species as shrubs *s.l.* including both dwarf-shrubs and shrubs.

Study Locations

The study was conducted in three locations spanning a 900 km (7.45°) latitudinal gradient from Dovrefjell in central Norway through Abisko in northern Sweden to Joatka in northern Norway (Figure 1). Joatka is the most continental location with the coldest winters, warmest summers, and shortest growing seasons (Table 1), whereas Dovrefjell has the coldest summers and warmest winters. All sites are very dry (Table 1). However, the up to 18-cm deep organic horizon in Dovrefjell should retain moisture better than the thin (max 4 cm) organic layer in Joatka. The study sites are situated in the forest–tundra ecotones. Mountain birch (*Betula pubescens* Ehrh. subsp. *tortuosa* (Ledeb.) Nyman) forms the treeline in all sites. In Dovrefjell, dense mountain birch forest forms a short, some hundreds of meters wide, transition from tundra. The forest–tundra ecotone in Abisko is a 3–4-km wide mosaic of mountain birch forest patches extending to tundra. In Joatka, discontinuous birch woodlands change to tundra above 400 m a.s.l. The forests in Abisko and Joatka are sparser com- pared to Dovrefjell, but the understorey in each location is dominated by the same dwarf-shrub species, *E. hermaphroditum* and *V. myrtillus*. Other common species in the forests are dwarf-shrubs blue heath (*Phyllodoce caerulea* (L.) Bab.) in Joatka, northern bilberry (*Vaccinium uliginosum* L.) in Abisko, and herbs such as goldenrod (*Solidago virgaurea* L.) and chickweed wintergreen (*Trientalis europaea* L.) in Dovrefjell. Wavy hair-grass (*Deschampsia flexuosa* (L.) Drejer) is a common forest species in all three locations, and the forest bottom layer consists of the bryophytes *Hylocomium splendens*, *Pleurozium schreberi*, and *Dicranum* spp. and a few lichens (for example, *Cladonia* spp.). The tundra vegetation is dominated by the shrubs *E. hermaphroditum*, *V. vitis- idaea*, and *B. nana*. Other common species in the tundra field layer are *V. uliginosum* in Joatka and Abisko, and bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.) and sheep's fescue (*Festuca ovina* (L.) in Dovrefjell. The bottom layer in the tundra is dominated by a moss *Rhytidium rugosum* in

Dovrefjell but by lichens, for example, *Cladonia mitis*, *Cetraria cucullata, Nephroma arctica* and a liverwort, *Ptilidium ciliare*, in Joatka and Abisko. The most abundant large herbivores in Dovrefjell are not only domesticated sheep but also wild reindeer (*Rangifer tarandus tarandus*) and moose (*Alces alces* L.) can occasionally graze in the forest– tundra ecotone. Study sites in Dovrefjell were fenced against ungulate herbivores. In Abisko and Joatka, semi-domesticated reindeer and moose are the large herbivore species. Smaller herbivores include mountain hares (*Lepus timidus* L.), willow grouse and ptarmigan (*Lagopus* spp.), lemmings (*Lemmus lemmus* L.), and voles (*Microtus* spp., *Clethrionomys* spp.), which are present in all study locations and were able to enter the study plots.

Experimental Design

At each of the three locations, two mountain birch forest patches and two tundra heath patches in the forest–tundra ecotone were selected as study sites in June–July 1998. Five control plots of 1 m^2 and five experimental warming plots were randomly set out in each of the four study sites, resulting in a total of 40 study plots per location: 20 in forest, 20 in tundra. The warming treatment was conducted using International Tundra Experiment (ITEX) hexagonal Open Top Chambers (hereafter OTC) (Marion and others 1997) with a maximum basal diameter of 146 cm. The chambers, standing at the plots year around, increased the surface air temperatures in July by between 0.8 and 2.5————————————C and annually by between 1.2 and 1.3————————————C in the tundra sites (Sjögersten and others 2003), which are within the range of what we expected based on other studies using OTC chambers (Arft and others 1999). These OTC chambers reduced the wind speed, especially in the tundra (Dalen 2004). The reduced wind speed in the chambers might cause larger increases in plant-experienced temperature than these air-temperature measurements (De Boeck and others 2012). Moreover, open top chambers could also influence snow and thaw depth (Bokhorst and others 2011b). These effects seem to be minor in the chambers used here because they advanced snowmelt only by 1–2 days. The chamber could also influence the grazing pressure from the major herbivores (microtine rodents and reindeer). Microtine rodents can enter the OTCs, but there were no significant differences in the frequency of signs of small rodents in warmed and control plots. The chambers will cer- tainly have excluded reindeer, but excluding rein- deer by exclosures in the close proximity to the chambered plots had no significant effect on the plant traits measured herein (JO pers. obs.). Excluding reindeer only increased the abundance of *B. nana* and reindeer lichens (Olofsson and others 2009), but the effect of the exclosures on *B. nana* was much smaller than the effects of the OTCs. We thus believe that the major differences between the chambers and the control plots are due to the warming effect although several of the mentioned treatment artifacts could also potentially influence the plants. Such influences, however, would be consistent across all chambered plots.

Vegetation Sampling and Measurements

Plant community composition in each location was recorded for the first time in July–August 1999 (after one year of warming), and for the second time in Abisko and Joatka in July 2009 (after 11 years of warming) and in Dovrefjell in July 2010 (after 12 years of warming). The point intercept method was used with a total of 87 vertical pins systematically distributed along the three diagonals of hexagonal warming chambers (29 per diagonal) and with the same arrangement on the control plots. The height of the highest hit and total number of the hits per species per pin was recorded individually for each of the pins. For this study, the total number of hits normalized to hits per 100 pins is used as an estimate of shrub abundance. In mid-July 2006, after eight years of experimental warming, the tips (10 cm) of 5–10 shoots of *E. hermaphroditum* and *V. vitis-idaea* were sampled for nutrient analysis from each study plot (n = 120). Shoot tips of *V. myrtillus* were collected from forest plots (n = 60) and shoot tips of *B. nana* from tundra plots (n = 60). Samples were air dried and stored

in a dry dark place. Leaves were separated from stems in the laboratory, and all the leaf material from five control and five warming treatment plots was pooled together at site level to obtain the required amount of leaf material for chemical analysis. Pooled samples were ground to a fine powder using a ball mill and analyzed for carbon (C), nitrogen (N), phosphorus (P), condensed tannins, and total phenolics. Total C and N concentrations were determined using a Leco Carbon–Nitrogen Analyzer (Laboratory Equipment Corporation, Michigan, USA). The concentration of total P was measured by Kjelldahl digestion followed by automated colorimetric methods on a Lachat flow injection analyzer (Taylor 2000). Condensed tannins and total phenolics were extracted in 50% acetone, which enables withdrawal of not only water-soluble phenolics but also, more importantly, the total pool of polyphenolics, including the slowly degradable fraction with high protein complexation capacity. Tannins were then analyzed by a modification of the vanillin method (Broadhurst and Jones 1978), which utilizes the formation of colored complexes between vanillin and condensed tannins. Catechin was used as the standard, and the results are expressed as catechin-equivalents. Total phenolics were analyzed by oxidizing phenolate ions in alkaline solution while reducing ferric ions to the ferrous state. Formation of a Prussian Blue complex with a potassium ferricyanide reagent was then detected spectrophotometrically (Price and Buttler 1977). Tannic acid was used as the standard and results are expressed as tannic acid equivalents.

Statistical Analyses

Effects of location (Dovrefjell, Abisko, Joatka), habitat (forest, tundra), treatment (OTC, control), and their interactions on the abundance of *E. hermaphroditum* and *V. vitis-idaea* were tested by repeated-measures ANOVA with location and habitat nested within site (two per each habitat in each location). For *V. myrtillus* and *B. nana* only the effect of location was tested, as these species occurred mainly in one of the habitats. For N, P, condensed tannins, and total phenolics, similar nested three-way (*E. hermaphroditum* and *V. vitis-idaea*) and two-way (*V. myrtillus* and *B. nana*) ANOVA models, without repeated measures, were run for investigating the effect of location, habitat, and treatment (and their interactions) on the variability of these chemical traits. To sum the species- specific responses, abundance-weighted average chemical traits were calculated for shrub communities consisting of the four study species which form, on average, 80% of the field layer above-ground biomass. Relative abundance weighted chemical traits were calculated at each plot by the following formula:

$$trait_{comm} = \sum_{i=l}^{n} p_i^* trait_i$$

where *trait*$_{comm}$ is the weighted average of a chemical trait for shrub community in a plot, *pi* is the proportional abundance of shrub species *i* on the plot measured as hits of species *i* divided by total amount of hits for the shrubs at the plot, and *trait*$_i$ is the chemical trait in species *i.* Variance of community traits was tested for the effect of location, habitat, and treatment (and their interactions) by the nested three-way ANOVA with site as an error term. The model assumptions were checked by model diagnostic plots and square root or $\log_{10}$ +1 transformation was performed, if necessary, to meet the assumption of homogeneity of the variances (see further Tables 2, 3 and 4). Relationships between the chemical traits at the community level were tested by Pearson's correlation. All analyses were run in the R statistical environment (R development core team 2011).

Results

Plant Community Composition

Warming increased the density of three out of four species investigated (*B. nana, E. hermaphroditum* and *V. vitis-idaea*) (Figure 2; Table 2); for *E. hermaphroditum*, the significant location 9 treatment 9 year interaction reveals that the effect of warming differed between locations (Table 3). The warming treatment increased the density of *E.hermaphroditum* by greater than 200% in Dovrefjell and greater than 50% in Abisko in 11–12 years, whereas the effect of warming was minor in Joatka (Table 2). In forest habitats across the whole latitudinal gradient, *E. hermaphroditum* responded more rapidly to warming than the other species, which led to even stronger dominance by *E.hermaphroditum*, mainly at the expense of *V. myrtillus* (Figure 2). To our surprise, despite the very large increase in total biomass in tundra habitat in Dovrefjell, the structure of the shrub community remained practically unchanged, that is, all the species increased in a similar way (Figure 2). In tundra in Abisko, *B.nana* increased the most: whereas in tundra in Joatka, the greatest increase was found for *V. vitis-idaea* (Table 2). *E. hermaphroditum* was the most abundant shrub species throughout all the study sites, also after 11-12 years warming; however, in tundra habitats in Abisko and Joatka, it responded weakly to warming relative to *B. nana* and *V. vitis-idaea*, and hence its dominance declined (Figure 2). The significant location 9 habitat interaction (Table 3) shows that the density of *V. vitis-idaea* differed between forest and tundra, but the difference was not consistent among locations; *V. vitis-idaea* was more abundant in the tundra in Joatka and Abisko and more abundant in the forest in Dovrefjell.

Nitrogen, Phosphorus, and Carbon

Both N (marginally significant, P = 0.054) and P (P = 0.006) concentrations of *B. nana* leaves were lower in warmed compared to control plots (Figure 3; Table 4), but did not differ in the other three shrub species between the treatments (Table 4; online Appendices 1–4). Owing to the decreased N and stable C concentrations (data not shown),C to N (C:N) and C to P (C:P) ratios in *B. nana* were significantly higher in the warmed plots compared to the controls (Table 4). Warming was associated with a reduced N:P ratio in *V.vitis-idaea*, but had no effect on the ratio in other species (Table 4). Nitrogen concentrations decreased with increasing latitudes in two of the dwarf-shrubs (*E. her-maphroditum* and *V. myrtillus*, Figure 4A). *Betula nana*, to the contrary, had high N concentrations at all locations, whereas *V. vitis-idaea* had the lowest N concentration in Abisko (Table 4; Figure 4A). Accordingly, C:N ratios of *E. hermaphroditum* and *V. myrtillus* increased with higher latitudes, whereas there were no clear patterns for B. nana and *V. vitis-idaea*. Phosphorus concentrations decreased with increasing latitude in all the shrubs; in *V. vitis-idaea*, there were, however, no differences between the two northernmost locations (Figure 4B). This resulted in rising C:P ratios for three out of four shrub species, whereas the C:P ratio of *V. vitis-idaea* remained unchanged in Abisko and Joatka. Deciduous shrubs have greater nutritional value (measured as N and P) compared to evergreen species. *V. vitis-idaea* consistently had the lowest nutrient concentrations at all locations (Figure 4A, B). When species were present in both habitats, they had higher concentrations of N and P, and consequently lower C:N and C:P ratios, in forest than tundra (Table 4). Generally, N:P ratios ranged between 6.9 and 12.7 among species across the latitudinal gradient. In *E. hermaphroditum* and *V. myrtillus* N:P ratios were not affected by location or habitat. In contrast, the significant habitat 9 location interaction for *V. vitis-idaea* reveals that N:P ratios are higher in tundra than in forest in the two northern locations (Abisko and Joatka), but lower in tundra than in forest in the

southern one (Dovrefjell). *Betula nana* had a significantly lower N:P ratio in Dovrefjell compared to the other two locations (Table 4).

Defense Compounds

Condensed tannin concentrations increased toward the north, across the latitudinal gradient, in *V. myrtillus*, *B. nana*, and *V. vitis-idaea*, but not in *E. hermaphroditum* (Table 4; Figure 4C). *Betula nana* had higher concentrations of both condensed tannins and total phenolics compared to the other shrub species, but there were substantial variations between the locations and within the species. The two evergreen species had higher tannin concentrations in the forest compared to tundra (Table 4; Figure 4C) although the large differences in tannin concentrations among species, locations, habitats, and warming treatment appear idiosyncratic (Table 4; Figure 4C). For example, the two deciduous shrubs responded in opposite ways to warming; tannin concentration decreased in *V. myrtillus* and increased in *B. nana* in Dovrefjell and Abisko, whereas it showed the opposite pattern in Joatka. Total phenolic concentration of deciduous shrubs increased with higher latitudes, whereas it decreased in *E. hermaphroditum* and showed no significant differences for *V. vitis-idaea* (Table 4; Figure 4D). Warming had no effect on total phenolics, except in *E. hermaphroditum*, which had higher concentrations of total phenolics in OTCs compared to controls in forest (16.3 ± 0.61 and 14.5 ± 1.05, mean ± SE, Table 4).

Weighted Average Community-Level Traits

The effect of warming on community-level N concentration depended on location and habitat, but was either negative or neutral. In contrast to the minor and mainly non-significant changes within species, warming decreased P concentrations of the whole community across the latitudinal gradient (Table 5). N and P concentrations of shrub communities were consistently higher in the forests than in tundra (Figure 5A). There was also a trend of decreasing N and P concentrations toward the north for the whole shrub community, similar to the trend found for the individual species (Figure 5A; Table 5). The level of condensed tannins in shrub communities responded idiosyncratically to warming and varied among habitats and locations (Table 5; Figure 5B). The concentrations of condensed tannins increased in both habitats in Dovrefjell, decreased in the forest in Abisko, and increased in forest in Joatka; they were unaffected by warming in the tundra in Abisko and Joatka.

Although total phenolic concentration of individual shrub species was not significantly influenced by warming (Table 3), we observed site-specific community-level changes in phenolic concentrations (Figure 5B; Table 5): Total phenolics of the shrub community increased in the forest and decreased in the tundra in Dovrefjell, showed no significant effects in Abisko, and increased in both habitats in Joatka (Figure 5B; Table 5). Nitrogen and P concentrations (r = 0.92), as well as condensed tannins and total phenolics (r = 0.51), were positively correlated, whereas C and N (r = -0.38), C and P (r = -0.28), C and tannins (r = -0.39), and N and phenols (r = -0.26) were negatively correlated.

Discussion

The composition of vascular plant communities in the locations investigated responded strongly to the warming experiment with large increases in plant biomass and shifts in community composition, whereas the changes in plant chemistry of the individual study species were more modest. This is in agreement with the results from previous studies (Welker and others 2005; Walker and others 2006; Aerts and others 2009; Elmendorf and others 2012). However, because our study combined measurements of plant abundance and chemistry, it provides novel information about the ecosystem-level con- sequences of these changes. In particular, the large differences in nutrient and

secondary metabolite concentrations among species imply that the changes in community composition rather than plant chemistry will drive the impacts of climate change on nutrient cycling and food availability for herbivores. Our experimental design also allowed us to address, for the first time, the effects of global warming on plant abundance and chemistry simultaneously in contrasting habitats across a latitudinal transect. In contrast to our hypothesis, and patterns arising from previous meta-analyses from tundra have documented (Walker and others 2006; Elmendorf and others 2012), deciduous shrubs did not consistently gain more from warming than evergreens. Moreover, also in contrast to our hypothesis, foliar N and P decreased, if they responded at all, to the warming treatment. Finally, our results highlight the idiosyncratic nature of CBSCs varying greatly within and among species and habitats and responding inconsistently to warming; a result in line with (Graglia and others (2001)).

Plant Community Composition

The field layer vegetation responded differently to warming in forest and tundra, as well as at the locations across the latitudinal gradient. The boundary between the closed forest and the tundra is a distinct ecotone, influencing the physical conditions as well as the distribution of species, including the field layer vegetation (Hofgaard and Wilmann 2002). Because tundra-growing *B. nana* increased dramatically, whereas *V. myrtillus*, occurring only in the forests, did not respond to warming, the initial differences in community composition led to opposing effects of warming on community structure with increased dominance of *E. hermaphroditum* in the forest and decreased dominance in the tundra. The responsiveness of B. nana has also been documented in earlier studies (Wahren and others 2005; Walker and others 2006), probably due to its ability to promote long shoot production from axillary buds in benign conditions (Bret-Harte and others 2001). Although deciduous shrubs, including *V. myrtillus*, are generally reported to increase in warming experiments (Walker and others 2006; Elmendorf and others 2012), there are good reasons why *V. myrtillus* should respond more slowly to warming than *B. nana. V. myrtillus* lacks the ability to produce long shoots from axillary buds and it is dependent on a permanent snow cover during winter because it is more sensitive to frost damage and winter warming events than other shrubs(Havas1971;Bokhorstand others 2011a). The positive effect of increased summer temperatures on the growth of *V. myrtillus* can thus be offset by a negative effect of earlier snow- melt in the warming treatment. Only very modest increases of *V. myrtillus* have indeed been reported from earlier studies (Rinnan and others 2009). The effect of warming on the plant community composition decreased with increasing latitude, with the largest growth increments in Dovrefjell, which is characterized by thick organic soil horizons and a relatively long growing season. By contrast, in Joatka, vegetation responsiveness to warming was probably hindered by the short and warm growing season and dry soils due to a thin organic layer on top of the well-drained gravely sandy soils. The positive relationship between the responsiveness of the vegetation and the moisture regime (Arft and others 1999; Walker and others 2006; Elmendorf and others 2012), as well as the more rapid increase in cover of shrubs in alpine than in low arctic sites (Walker and others 2006), are consistent with patterns revealed in meta-analyses and shows that differences across our relatively dry environmental gradients within the Scandinavian tundra follow the same patterns expected from larger global gradients (Walker and others 2006).

Plant Chemistry

Plant nutrient concentrations vary greatly among species. Deciduous species *V. myrtillus* and *B. nana* had consistently higher foliar N and P concentrations than evergreens *E. hermaphroditum* and *V. vitis-idaea*. By contrast, effects of warming were small, mostly insignificant, and predominantly negative. The net effect of warming on plant nutrient concentration should be a result of a positive impact via increased soil nutrient availability (Welker and others 2005) and a negative impact via

dilution from accelerated growth (Aerts and others 2009) and advanced phenology (Torp and others 2010). These processes seemed broadly to balance each other out in three of the study species, whereas the negative effects seem to be more important for *B. nana*. The consistently higher nutrient concentration in the forest than in the tundra is probably an effect of shading from the trees (Hansen and others 2005) although higher soil nutrient availability in the forest cannot be ruled out; indeed, there is evidence for substantially higher N mineralization (and NH_4^+-N availability) in forests at Abisko and Dovrefjell compared with tundra heaths (Sjögersten and Wookey 2005). On a global scale, plant leaf N and P concentrations increase from the equator toward the poles, level off at latitudes around 60° north, and sparse northern data points suggest a decrease at higher latitudes (Reich and Oleksyn 2004). Our results support this suggestion of a decreasing trend in foliar nutrient concentrations above 60° north. Also, results of foliar P concentrations for the same evergreen species along a subarctic elevational gradient in Abisko show a decreasing pattern toward higher altitudes, but this trend was not found for N along that gradient (Sundqvist and others 2011). Despite the large differences in phenol and tannin concentrations among species, locations, and habitats, the responses to warming treatment and environmental gradients seem to be idiosyncratic. This confirms the results from previous studies from the subarctic tundra (Graglia and others 2001; Hansen and others 2005; Torp and others 2010). It also shows that the plant allocation of C to phenols and tannins may vary as much among different sites in the Scandinavian tundra as previously reported between the Scandinavian and North American tundra (Graglia and others 2001). This pattern is obvious both at species and shrub community levels. Decreasing N:P ratios with increasing latitude may imply stronger N limitation in the north, which is in line with the general pattern shown in the meta-analysis by Elser and others (2007). The range of N:P ratios in our study species indicates that N and P are co-limiting the growth of shrubs in the Scandinavian forest–tundra ecotone.

Community-Weighted Average Traits and Possible Consequences for Ecosystem Processes

Nitrogen and P concentrations in the shrub com- munities were higher in the forest than in the tundra and decreased with higher latitudes. The weighted average trait approach reveals important and consistent changes that could not be detected at the species level. Stoichiometrical theory and empirical studies suggest that the nutritional quality of the primary producers should control the trophic structure of the ecosystems (Schmitz 2008; Cebrian and others 2009). The higher N and P concentration in forest, lower latitudes, and warmer plots could thus result in a higher efficiency of trophic transfer, resulting in higher consumer productivity and faster recycling of resources (Cebrian and others 2009). Moreover, the higher nutrient concentration of the living plants should also result in higher nutrient concentrations in plant litter (Soudzilovskaia and others 2007), and thus influence the nutrient cycling and carbon storage in the soil (Cornelissen and others 2007). However, the higher condensed tannin concentrations in evergreen dwarf-shrubs in the forest may counteract the positive effects of increased nutrient concentration, at least for herbivores for- aging on these plants. Increased evergreen dominance also suggests CBSC-rich litter inputs, and therefore slow nutrient turnover in forests. Other factors being equal, this should further favour evergreen shrubs over deciduous, and enhance C accumulation in recalcitrant litter in treeline forest soils. The differences in plant abundance-weighted traits are much larger than the relatively small differences in plant chemistry within species, and are driven primarily by the large changes in plant community composition and the substantial differences in plant chemistry among species. More specifically, the proportion of nutrient-rich deciduous shrubs is the major factor behind the variations in community-weighted N and P concentrations. Interestingly, however, the highly contrasting responses of the nutrient-rich deciduous shrubs do not transfer into the changes in the community-weighted traits. The only significant changes in chemistry due to warming, the negative effect on N and P

concentrations in *B. nana*, at least partly explain this. The importance of these changes for herbivores and further in the trophic chain will depend on herbivores' reliance on high quality plants. Reindeer have been shown to be dependent on high quality forage, and the changes recorded here could potentially have large effects on their body weight gain (White 1983; Cebrian and others 2009). However, because reindeer forage selectively on preferred food items changes in plant phenology or spatial variation may be as important as the average nutritional quality of the vegetation (Mårell and others 2006; Post and others 2009). Furthermore, future vegetation changes will be an interactive effect of future climate and grazing regimes (Post and Pedersen 2008; Olofsson and others 2009). Grazing could both hamper the advance of the forest–tundra zone (Aune and others 2011) and reduce the increase of deciduous shrubs in a warmer climate (Post and Pedersen 2008; Olofsson and others 2009; Hofgaard and others 2010) and thus reinforce the negative effect of future climate changes on average food quality.

Conclusions

The results from this experimental multisite study suggest that global warming will considerably re-shape tundra vegetation leading to increased plant abundance, but reduced nutrient concentrations. These alterations indicate more, but lower quality, plant litter, which potentially decelerates nutrient turnover and could thus mitigate climate warming in the longer term (Cornelissen and others 2007).

Moreover, our results also show that if treeline forests will advance in the future, the indirect effect of this rise could have greater effects on the eco- system processes than the direct effect of warming by increasing the nutrient concentrations in the understory and by changes in community composition and within-species chemistry. Both these results are important for understanding the cascading effect of changes in the tundra plant com- munity on herbivores and decomposers in the future.

Acknowledgements

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Legends to Figures:

Figure 1. Map of Scandinavia showing the study locations, Dovrefjell (Norway), Abisko (Sweden), and Joatka (Norway).

Figure 2. Proportional mean dwarf-shrub densities on the warmed plots (n = 10 per habitat in each location) in the beginning of the experiment and after 10–11 years warming. Data for control plots are presented in Table 2. Area of the pie describes the total dwarf-shrub density in number of hits per 100 pins.

Figure 3. Nitrogen and phosphorus concentrations in *B. nana* leaves in control and warmed plots. The points represent means of n = 6, and error bars are ±1 SE.

Figure 4. Foliar A nitrogen, B phosphorus, C condensed tannins, and D total phenolic concentrations in shrub species along the latitudinal gradient from Dovrefjell to Joatka. Only statistically significant differences are shown in this figure; a detailed presentation is available in online Appendices 1–4. For nitrogen and phosphorus, the points represent mean values of n = 4; for tannins, mean values of n = 2; and for the phenolics mean values of n = 4 for *B. nana* and *V. myrtillus* and of n = 8 for *E. hermaphroditum* and *V. vitis-idaea*. Error bars represent ±1 SE. Tannin concentrations are expressed as tannic acid and phenols as catechin equivalents.

Figure 5. Abundance- weighted shrub community nitrogen and phosphorus concentrations (A) and condensed tannin and total phenolic concentrations (B) along the latitudinal gradient. The points represent the means of five plot-scale communities and error bars are ±1 SE. Note In figure (A) phosphorus values were multiplied by 10. The data is presented in bar graph form in the online Appendix 5.
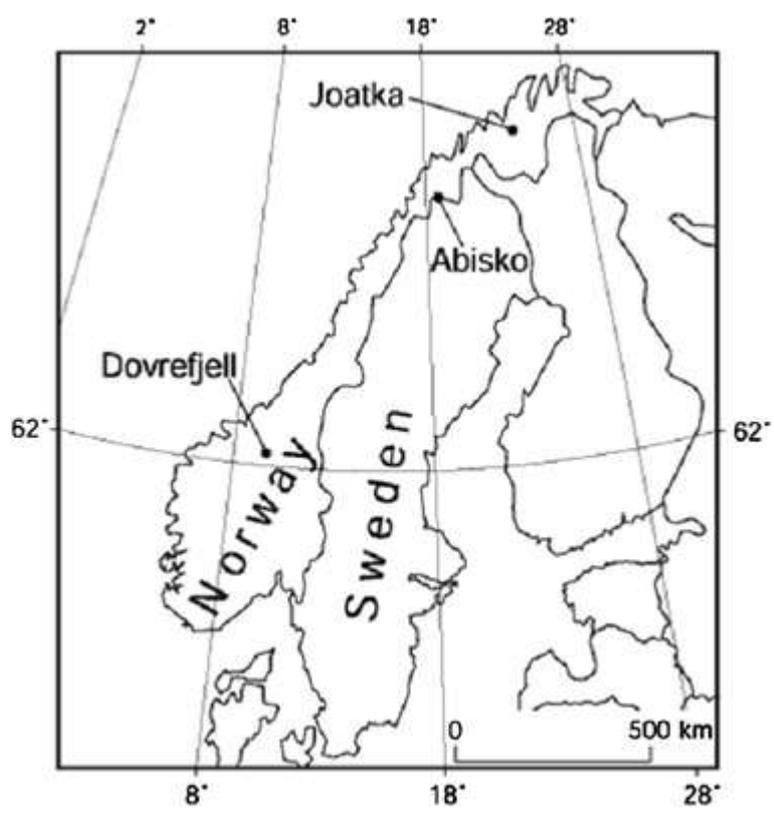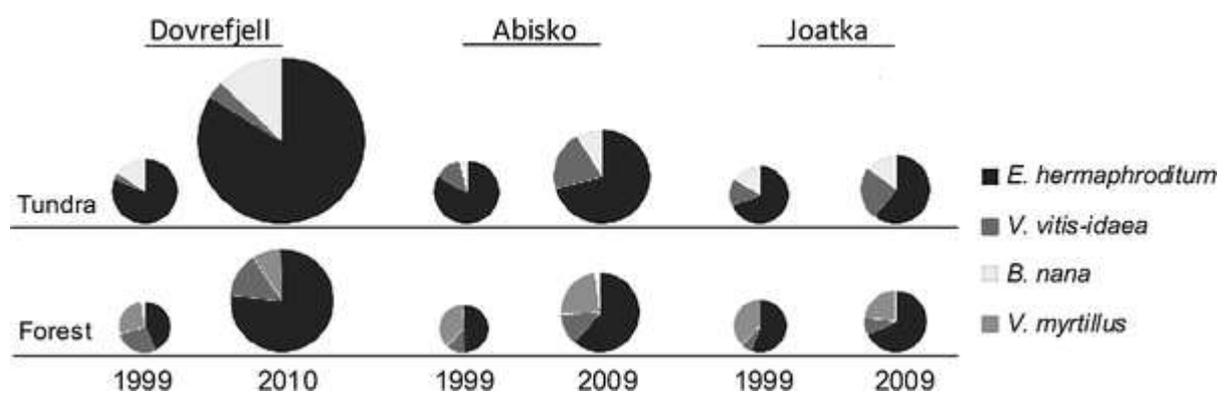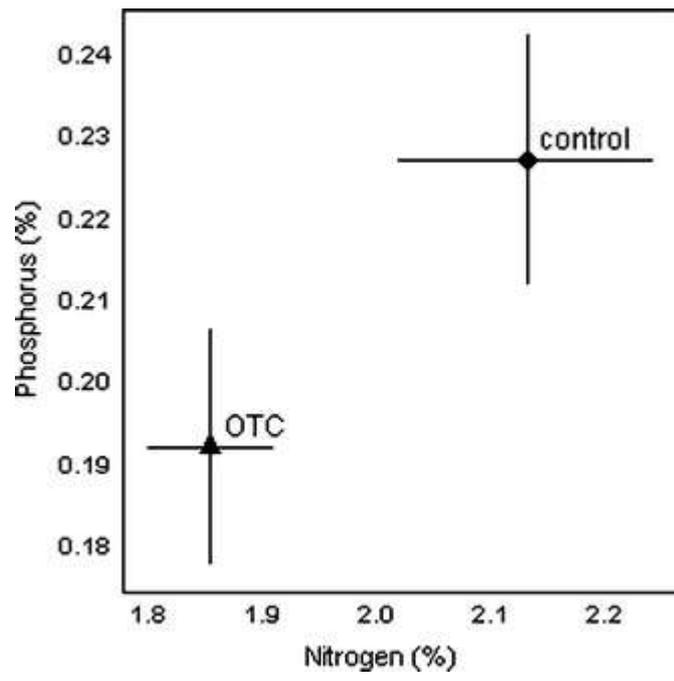
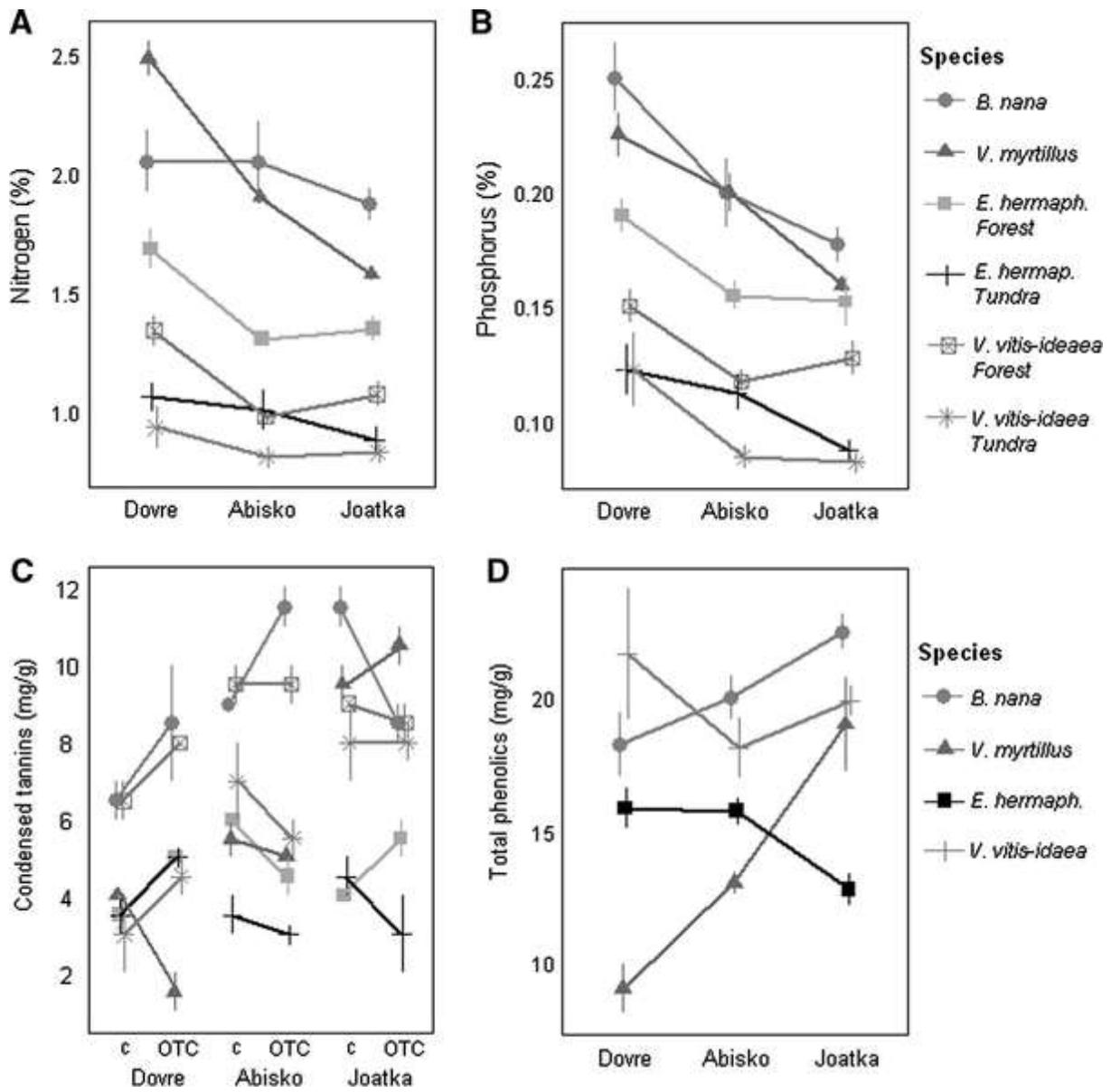Figure 1

Figure 2.

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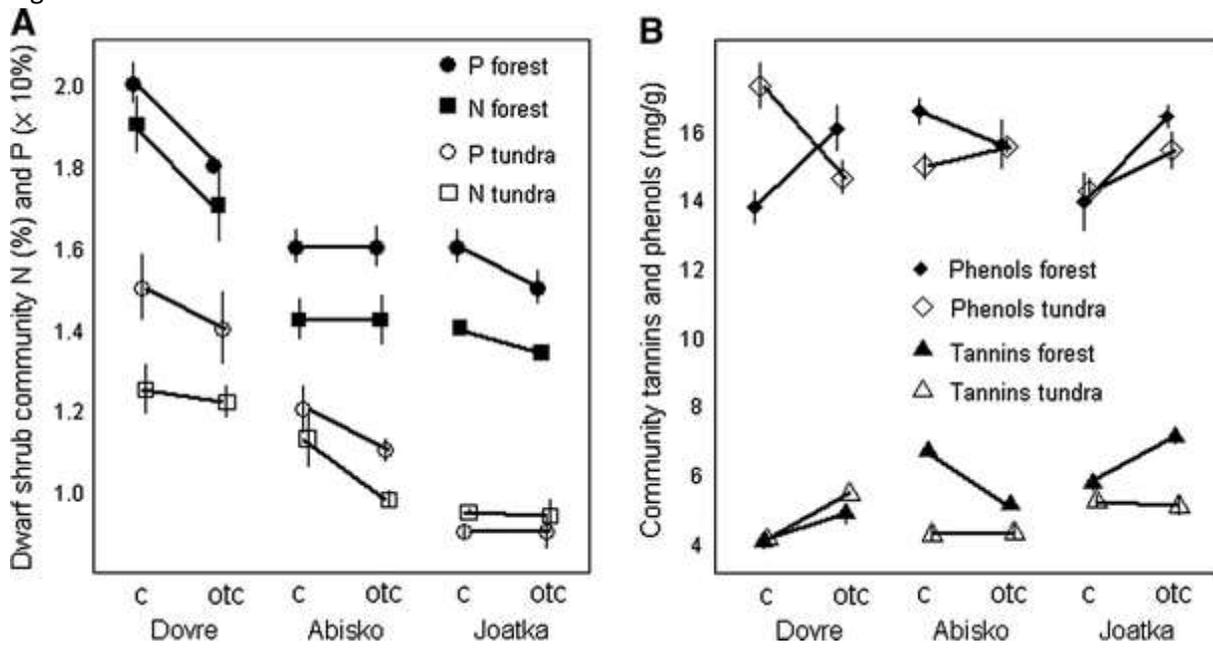
Tables:

Table 1 Site Characteristic of the Study Locations

	Dovrefjell	Abisko	Joatka
Location	62.30°N; 9.62°E	68.31°N; 18.86°E	69.75°N; 23.99°E
Altitude (m a.s.l.)	1,000–1,100	520–600	420–500
Mean annual temp (°C)	0.24	−0.79	−2.42
Mean July temp (°C)	10.6	11.3	12.0
Mean January temp (°C)	−6.9	−9.7	−12.4
Annual precipitation (mm)	449	338	443
Growing degree days (3°C)	140	138	124
Soil pH	4.4	4.0	3.5
Soil organic horizon depth (cm)	0–18	0–7	0–4
Soil total N (mg/g)			
Forest	19.2	14.0	14.6
Tundra	16.7	13.3	15.1
Soil total P (mg/g)			
Forest	1.03	0.91	0.80
Tundra	0.96	0.90	1.05

Climate data for the study period of 1998–2010 from Abisko Scientific Research Station and www.met.no.

Dovrefjell Fokstugu meteorological station at 937 m a.s.l., 27 km south of the study site. **Abisko** Abisko Research Station at 385 m a.s.l., 4 km north of the study site. **Joatka** Temperature from Suolovuopmi and Suolovuopmi-Lulit stations at 380 m a.s.l., 25 km southwest of the study site, precipitation from Joatkajavre station (1999–2006) 1 km from the study sites. Mean annual temperatures were adjusted to the mean altitudes of study sites by converting with lapse rate of −0.6°C/100 m from values for respective meteorological stations. GDD3-values from Dalen and Hofgaard (*2005*) from period 1971 to 2000. Soil data from Sjögersten and others (*2003*), averages for five control plots, five cores from 0 to 2 cm depth per plot.

Table 2
Shrub Abundance Measured in Hits per 100 Pins in 1999 and After 10–11 Years of Warming in Three Locations and Two Habitats

	Year	Dovrefjell[1]				Abisko			
		Forest		Tundra		Forest		Tundra	
		Control	OTC	Control	OTC	Control	OTC	Control	OTC
E. hermaphroditum	1999	37.3 ± 10.0	29.4 ± 4.6	78.2 ± 4.2	92.0 ± 9.9	32.7 ± 7.1	32.2 ± 8.4	106.5 ± 9.5	92.7 ± 10.0
	2009	**51.5 ± 13.4**	**211.9 ± 32.7**	**197.5 ± 16.2**	**590.8 ± 38.8**	42.6 ± 8.9	99.1 ± 28.2	**132.2 ± 17.7**	**168.8 ± 15.5**
V. vitis-idaea	1999	9.7 ± 2.6	17.7 ± 1.3	0.8 ± 0.5	2.8 ± 1.1	6.2 ± 0.8	7.5 ± 1.7	9.8 ± 3.2	14.3 ± 3.0
	2009	**12.1 ± 3.8**	**38.1 ± 11.2**	**6.4 ± 2.6**	**22.8 ± 6.1**	16.0 ± 2.1	20.2 ± 5.1	**20.4 ± 5**	**47.0 ± 6.5**
V. myrtillus	1999	24.2 ± 4.8	18.4 ± 4.5	0 ± 0	0 ± 0	24.7 ± 3.8	23.3 ± 5.1	0 ± 0	0 ± 0
	2009	29.9 ± 7.6	24.2 ± 7.8	0 ± 0	0 ± 0	22.5 ± 6.1	38.2 ± 11.5	0.2 ± 0.2	0.2 ± 0.2
B. nana	1999	0.3 ± 0.3	1.5 ± 1.5	21.9 ± 5.0	18.0 ± 23.0	0 ± 0	0.7 ± 0.6	3.1 ± 1.4	4.2 ± 1.5
	2009	0 ± 0	1.7 ± 1.1	**57.5 ± 13.7**	**90.4 ± 12.3**	0 ± 0	3.2 ± 2.2	**9.4 ± 3.2**	**20.9 ± 4.1**

[1]In Dovrefjell the second vegetation survey was done in 2010.

Values in bold indicate the significant ($P < 0.05$) time × treatment interaction in each habitat and location combination.

Table 3
Summary of ANOVA Results for Shrub Abundance

	E. hermaphroditum [1]		V. vitis-idaea [1]		B. nana [2]		V. myrtillus [2]	
	F_{df}	P	F_{df}	P	F_{df}	P	F_{df}	P
Error: site								
Location	$13.63_{2,5}$	**0.009**	$4.67_{2,5}$	0.071	$8.79_{2,2}$	0.102	$0.20_{2,3}$	0.830
Habitat	$57.67_{1,5}$	**<0.001**	$1.49_{1,5}$	0.276				
Location*habitat	$5.93_{2,5}$	**0.048**	$20.23_{2,5}$	**0.004**				
Error: site/plot								
Treatment	$37.84_{1,101}$	**<0.001**	$19.14_{1,101}$	**<0.001**	$13.07_{1,50}$	**<0.001**	$0.15_{1,51}$	0.699
Location*treatment	$19.45_{2,101}$	**<0.001**	$4.65_{2,101}$	**0.011**	$0.74_{2,50}$	0.48	$2.17_{2,51}$	0.124
Habitat*treatment	$0.00_{1,101}$	0.991	$1.87_{1,101}$	0.175				
Location*habitat*treatment	$1.67_{2,101}$	0.192	$1.82_{2,101}$	0.167				
Error: within								
Year	$148.73_{1,107}$	**<0.001**	$47.41_{1,107}$	**<0.001**	$9.93_{1,53}$	**0.003**	$0.02_{1,54}$	0.887

	E. hermaphroditum [1]		V. vitis-idaea [1]		B. nana [2]		V. myrtillus [2]	
	F_{df}	P	F_{df}	P	F_{df}	P	F_{df}	P
Location*year	$49.47_{2,107}$	**<0.001**	$2.9_{2,107}$	0.060	$24.04_{2,53}$	**<0.001**	$0.32_{2,54}$	0.727
Habitat*year	$7.26_{1,107}$	**0.008**	$5.13_{1,107}$	**0.025**				
Treatment*year	$55.54_{1,107}$	**<0.001**	$5.96_{1,107}$	**0.016**	$14.72_{1,53}$	**<0.001**	$0.23_{1,54}$	0.630
Location*habitat*year	$9.20_{2,107}$	**<0.001**	$0.32_{2,107}$	0.729				
Location*treatment*year	$15.43_{2,107}$	**<0.001**	$0.14_{2,107}$	0.868	$1.71_{2,53}$	0.192	$0.20_{2,54}$	0.822
Habitat*treatment*year	$0.02_{1,107}$	0.876	$2.12_{1,107}$	0.148				
Location*habitat*treatment*year	$0.82_{2,107}$	0.445	$0.15_{2,107}$	0.858				

Transformations prior to modeling: [1]sqrt, [2]$\log_{10}(x + 1)$.

Values in bold indicate statistical significance at $P < 0.05$.

Table 4
Summary of ANOVA Models for Foliar Chemistry of Shrubs

	E. hermaphroditum		V. vitis-idaea		V. myrtillus [1,2]		B. nana [1]	
	F	P	F	P	F	P	F	P
Nitrogen								
Location	$8.50_{2,6}$	**0.018**	$8.68_{2,6}$	**0.017**	$80.90_{2,3}$	**0.002**	$0.42_{2,3}$	0.691
Habitat	$69.69_{1,6}$	**<0.001**	$30.34_{1,6}$	**0.002**				
Location*habitat	$3.01_{2,6}$	0.124	$2.00_{2,6}$	0.216				
Treatment	$2.60_{1,6}$	0.158	$0.85_{1,6}$	0.393	$0.46_{1,3}$	0.545	$9.47_{1,3}$	*0.054*
Location*treatment	$0.74_{2,6}$	0.517	$1.05_{2,6}$	0.406	$3.66_{2,3}$	0.157	$0.02_{2,3}$	0.982
Habitat*treatment	$0.05_{1,6}$	0.833	$0.70_{1,6}$	0.434				
Location*habitat*treatment	$1.69_{2,6}$	0.261	$0.73_{2,6}$	0.520				
Phosphorus								
Location	$7.66_{2,6}$	**0.022**	$19.69_{2,6}$	**0.002**	$12.87_{2,3}$	**0.034**	$9.06_{2,3}$	*0.054*
Habitat	$58.33_{1,6}$	**<0.001**	$49.00_{1,6}$	**<0.001**				

	E. hermaphroditum		V. vitis-idaea		V. myrtillus [1,2]		B. nana [1]	
	F	P	F	P	F	P	F	P
Location*habitat	$1.08_{2,6}$	0.397	$1.08_{2,6}$	0.397				
Treatment	$1.25_{1,6}$	0.306	$0.20_{1,6}$	0.670	$0.02_{1,3}$	0.907	$49.00_{1,3}$	**0.006**
Location*treatment	$0.24_{2,6}$	0.796	$1.74_{2,6}$	0.254	$0.53_{2,3}$	0.633	$1.00_{2,3}$	0.465
Habitat*treatment	$0.20_{1,6}$	0.670	$0.80_{1,6}$	0.406				
Location*habitat*treatment	$0.39_{2,6}$	0.695	$0.91_{2,6}$	0.451				
N:P ratio								
Location	$1.47_{2,6}$	0.302	$4.19_{2,6}$	0.073	$1.15_{2,3}$	0.427	$47.82_{2,3}$	**0.005**
Habitat	$1.70_{1,6}$	0.241	$4.41_{1,6}$	0.081				
Location*habitat	$0.92_{2,6}$	0.447	$11.27_{2,6}$	**0.009**				
Treatment	$0.00_{1,6}$	0.993	$9.97_{1,6}$	**0.020**	$0.15_{1,3}$	0.721	$0.25_{1,3}$	0.654
Location*treatment	$1.15_{2,6}$	0.377	$2.48_{2,6}$	0.164	$0.01_{2,3}$	0.993	$0.04_{2,3}$	0.957
Habitat*treatment	$0.06_{1,6}$	0.809	$1.54_{1,6}$	0.261				

	E. hermaphroditum		V. vitis-idaea		V. myrtillus [1,2]		B. nana [1]	
	F	P	F	P	F	P	F	P
Location*habitat*treatment	$0.38_{2,6}$	0.701	$1.98_{2,6}$	0.218				
C:N ratio								
Location	$5.52_{2,6}$	**0.044**	$5.24_{2,6}$	**0.048**	$110.06_{2,3}$	**0.002**	$0.60_{2,3}$	0.603
Habitat	$61.77_{1,6}$	**<0.001**	$30.40_{1,6}$	**0.001**				
Location*habitat	$1.34_{2,6}$	0.331	$0.67_{2,6}$	0.549				
Treatment	$3.63_{1,6}$	0.105	$1.13_{1,6}$	0.329	$0.55_{1,3}$	0.511	$18.97_{1,3}$	**0.022**
Location*treatment	$2.22_{2,6}$	0.190	$0.91_{2,6}$	0.453	$3.38_{2,3}$	0.171	$0.22_{2,3}$	0.816
Habitat*treatment	$0.20_{1,6}$	0.669	$0.12_{1,6}$	0.743				
Location*habitat*treatment	$2.59_{2,6}$	0.154	$0.75_{2,6}$	0.511				
C:P ratio								
Location	$5.65_{2,6}$	**0.042**	$22.34_{2,6}$	**0.002**	$17.67_{2,3}$	**0.022**	$8.42_{2,3}$	*0.059*
Habitat	$39.96_{1,6}$	**<0.001**	$84.00_{1,6}$	**<0.001**				

	E. hermaphroditum		V. vitis-idaea		V. myrtillus [1,2]		B. nana [1]	
	F	P	F	P	F	P	F	P
Location*habitat	$1.81_{2,6}$	0.243	$4.33_{2,6}$	*0.069*				
Treatment	$2.35_{1,6}$	0.177	$0.09_{1,6}$	0.780	$0.04_{1,3}$	0.862	$24.16_{1,3}$	**0.016**
Location*treatment	$1.12_{2,6}$	0.385	$1.36_{2,6}$	0.325	$0.64_{2,3}$	0.588	$0.61_{2,3}$	0.598
Habitat*treatment	$0.13_{1,6}$	0.727	$0.54_{1,6}$	0.491				
Location*habitat*treatment	$0.61_{2,6}$	0.610	$1.36_{2,6}$	0.326				
Condensed tannins								
Location	$0.00_{2,6}$	1.000	$18.88_{2,6}$	**0.003**	$108.50_{2,3}$	**0.002**	$6.53_{2,3}$	0.081
Habitat	$10.29_{1,6}$	**0.018**	$37.50_{1,6}$	**<0.001**				
Location*habitat	$3.43_{2,6}$	0.102	$4.63_{2,6}$	0.061				
Treatment	$0.67_{1,6}$	0.445	$0.33_{1,6}$	0.585	$8.00_{1,3}$	*0.066*	$1.00_{1,3}$	0.391
Location*treatment	$12.67_{2,6}$	**0.007**	$5.58_{2,6}$	**0.043**	$18.50_{2,3}$	**0.021**	$12.33_{2,3}$	**0.036**
Habitat*treatment	$2.67_{1,6}$	0.154	$0.33_{1,6}$	0.585				

	E. hermaphroditum		V. vitis-idaea		V. myrtillus [1,2]		B. nana [1]	
	F	P	F	P	F	P	F	P
Location*habitat*treatment	$8.67_{2,6}$	**0.017**	$1.08_{2,6}$	0.397				
Total phenolics								
Location	$7.26_{2,6}$	**0.025**	$1.25_{2,6}$	0.352	$33.61_{2,3}$	**0.009**	$24.33_{2,3}$	**0.014**
Habitat	$2.71_{1,6}$	0.151	$0.26_{1,6}$	0.630				
Location*habitat	$0.33_{2,6}$	0.734	$4.52_{2,6}$	0.063				
Treatment	$0.81_{1,6}$	0.404	$1.15_{1,6}$	0.326	$1.06_{1,3}$	0.379	$4.12_{1,3}$	0.135
Location*treatment	$1.97_{2,6}$	0.220	$0.09_{2,6}$	0.916	$2.15_{2,3}$	0.264	$0.46_{2,3}$	0.668
Habitat*treatment	$9.32_{1,6}$	**0.022**	$0.92_{1,6}$	0.375				
Location*habitat*treatment	$2.94_{2,6}$	0.129	$0.66_{2,6}$	0.551				

Data $\log_{10}(x + 1)$ transformed prior to modeling of [1]nitrogen data, [2]phosphorus and total phenolics data.

Values in italic indicate statistical significance at $P < 0.1$ and in bold significance at $P < 0.05$.

Table 5
Summary of ANOVA Models for Weighted Average Traits for the Whole Dwarf-Shrub Community

	Nitrogen			Phosphorus			Tannins			Phenolics		
	df	F	P	df	F	P	df	F	P	df	F	P
Error: site												
Location	2	8.36	**0.025**	2	7.87	**0.029**	2	8.27	**0.026**	2	0.179	0.841
Habitat	1	34.88	**0.002**	1	27.76	**0.003**	1	12.42	**0.017**	1	0.007	0.935
Treatment	1	0.02	0.902	1	0.19	0.678	1	4.8	0.08	1	0.816	0.408
Location*habitat	2	0.92	0.456	2	0.11	0.895	2	5.54	0.054	2	0.44	0.667
Error: within												
Treatment	1	11.1	**0.001**	1	14.03	**<0.001**	1	8.09	**0.005**	1	4.135	**0.045**
Location*treatment	2	1.82	0.167	2	2.57	0.082	2	28.08	**<0.001**	2	6.812	**0.002**
Habitat*treatment	1	0.85	0.359	1	0.61	0.436	1	1.22	0.272	1	9.685	**0.002**
Location*habitat*treatment	2	4.89	**0.009**	2	1.41	0.25	2	19.89	**<0.001**	2	15.557	**<0.001**

Values in bold indicate statistical significance at $P < 0.05$.