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Higher vascular plant abundance associated with decreased ecosystem respiration after 20 years of warming in the forest–tundra ecotone

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Abstract

1. The on-going climate warming is promoting shrub abundance in high latitudes, but the effect of this phenomenon on ecosystem functioning is expected to depend on whether deciduous or evergreen species increase in response to warming.

2. To explore effects of long-term warming on shrubs and further on ecosystem functioning, we analysed vegetation and ecosystem CO_2 exchange after 20 years of warming in the forest–tundra ecotone in subarctic Sweden. A previous study conducted 9 years earlier had found increased evergreen *Empetrum nigrum* ssp. *hermaphroditum* in the forest and increased deciduous *Betula nana* in the tundra.

3. Following current understanding, we expected continued increase in shrub abundance that would be stronger in tundra than in forest. We expected warming to increase *ecosystem respiration* (R_e) and *gross primary productivity* (GPP), with a greater increase in R_e in tundra due to increased deciduous shrub abundance, leading to a less negative *net ecosystem exchange* and reduced ecosystem C sink strength.

4. As predicted, vascular plant abundances were higher in the warmed plots with a stronger response in tundra than in forest. However, whereas *B. nana* had increased in abundance since the last survey, *E. hermaphroditum* abundance had declined due to several moth and rodent outbreaks during the past decade. In contrast to predictions, R_e was significantly lower in the warmed plots irrespective of habitat, and GPP increased marginally only in the forest. The lower R_e and a higher GPP under warming in the forest together led to increased net C sink. R_e was negatively associated with the total vascular plant abundance.

5. Our results highlight the importance of disturbance regimes for vegetation responses to warming. Climate warming may promote species with both a high capacity to grow under warmer conditions and a resilience towards herbivore outbreaks. Negative correlation between R_e and total vascular plant abundance

further indicate that the indirect impacts of increased plants on soil microclimate may become increasingly important for ecosystem CO_2 exchange in the long run, which adds to the different mechanisms that link warming and CO_2 fluxes in northern ecosystems.

1 | INTRODUCTION

The high latitudes of Earth are warming as much as four times faster than the global average (Rantanen et al., 2022), which is drastically changing the plant community structure and functioning of ecosystems in these areas (Wookey et al., 2009). The most important plant group responding to warming are the shrubs, which have increased in height as well as expanded their distribution along both latitudes and altitudes—the process generally known as *Arctic shrubification* or *greening* (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012; Myers-Smith et al., 2011, 2020).

Vegetation composition plays a major role in ecosystem processes (Bråthen et al., 2017; Wookey et al., 2009). Increased growing season temperatures together with faster nutrient cycles facilitate shrub growth (Bjorkman et al., 2020; Zamin & Grogan, 2012), leading into greater *gross primary productivity* (GPP) and carbon uptake from the atmosphere (Cahoon et al., 2012; Hobbie & Chapin III, 1998; Shaver et al., 2007). In the long term, however, warming-induced vegetation change can modify ecosystem CO_2 fluxes through several indirect mechanisms over and above the direct effects (Weintraub & Schimel, 2005; Wookey et al., 2009). Taller and darker shrub vegetation reduces albedo (Blok et al., 2011) and increases accumulation of snowpacks (Way & Lapalme, 2021), which both can lead to higher wintertime soil temperatures (Leffler & Welker, 2013), N mineralization (DeMarco et al., 2011) and *ecosystem respiration* (R_e) (Nobrega & Grogan, 2007). These effects may accelerate decomposition of soil organic matter (SOM) and lead to increased rates of R_e (Nobrega & Grogan, 2007), thus contributing to a greater CO_2 release from tundra (Biasi et al., 2008; Cahoon et al., 2012; Väisänen et al., 2014). If climate warming accelerates R_e more than GPP, *net ecosystem exchange* (NEE) is reduced, which induces more carbon losses from the ecosystem (Bradford et al., 2016). However, the amplitude of shrubification and the dynamics between vegetation and carbon sink are not straightforward but rather a sum of complex site- and time-dependent interactions (Mekonnen et al., 2021). For example, although shrubification may increase soil temperatures, the taller and denser vegetation cover may also buffer the soil against warming during peak summer season through increased shading (Blok et al., 2010), and it is not yet fully understood whether shrubification eventually results in positive or negative temperature feedbacks (Way & Lapalme, 2021).

It has been hypothesized that one key predictor in the effect of Arctic shrubification on carbon cycling is whether warming increases deciduous or evergreen dwarf shrubs (Vowles & Björk, 2018). The expansion of shrubs has often been attributed to an increase in deciduous species such as willows (*Salix* sp.) and dwarf birch, *Betula nana* (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012; Myers-Smith et al., 2011). These species can enhance soil respiration through producing easily decomposing litter and having ectomycorrhizal fungal symbionts that efficiently decompose SOM (Parker et al., 2021). In contrast, evergreen dwarf shrubs have lower GPP and respiration rates, store greater amount of nutrients in long-lived shoots, leaves and roots and thus decelerate carbon cycles (Vowles & Björk, 2018 and references therein). In particular, the evergreen dwarf shrub *Empetrum nigrum* ssp. *hermaphroditum* (hereafter *E. hermaphroditum*), one of the most common plant species found in Fennoscandian subarctic environments, produces slowly decomposing litter with high concentrations of allelopathic compounds that can decelerate soil nutrient and carbon cycles (Bråthen et al., 2017). Increased abundance of *E. hermaphroditum* in response to climate warming (Stark et al., 2021; Vuorinen et al., 2017) could thus lead to slower rather than faster carbon cycles (Vowles & Björk, 2018).

Here, we examine whether longer-term changes in vegetation differ from shorter-term changes, and whether the effects of warming on CO_2 exchange differ between tundra and forest due to the different response of deciduous and evergreen dwarf shrubs to warming. For this, we report the responses of plant species composition and ecosystem CO_2 fluxes to 20 years of simulated climate warming, carried out using open top chambers (hereafter OTCs) at tundra and mountain birch forest sites located in the forest–tundra ecotone in northernmost Sweden. Results from the same study sites 9 years earlier showed that although *E. hermaphroditum* is the dominant species in both forest and tundra, its abundance had increased in response to warming in forest only, while *B. nana* had increased in tundra (Kaarlejärvi et al., 2012), making this an optimal setting to test the influence of these species on the response of CO_2 fluxes to warming (Figure 1).

We predict that (H1) the effect of warming on dwarf shrub growth will be generally stronger in tundra than forest because the deciduous *B. nana* is able to effectively respond to improved growing conditions (Bret-Harte et al., 2001) and because shrub growth is potentially more temperature limited in tundra than forest (Sundqvist

et al., 2020). As found in earlier warming experiments (Biasi et al., 2008, Väisänen et al., 2014,), we predict that (H2) warming will increase GPP and R_e both in the forest and the tundra, but owing to the positive effects of increased *B. nana* abundance on R_e (Vowles & Björk, 2018), the increase in R_e will be stronger in tundra than forest. Finally, we predict that (H3) in tundra the effect of warming on R_e will be stronger than on GPP, thus leading to a reduced ecosystem C sink strength (manifested as less negative NEE), whereas in forest, no difference, or even increased sink strength will be found.

2 | MATERIALS AND METHODS

2.1 | Study area and experimental design

The study area is in the forest–tundra ecotone—a 3- to 4-km wide mosaic of mountain birch forest patches extending to tundra. It is located in the oroarctic region (Virtanen et al., 2016), a few kilometres south of the Abisko Scientific Research Station in northernmost Sweden (68°21′ N, 18°49′ E). In the area, the forest and tundra sites are located at altitudes of 523 and 616 m a.s.l. respectively. The mean annual temperature in the period 1960–1990 was −0.2°C (Callaghan et al., 2013) and in the period 1991–2018 was 0.7°C (Abisko Scientific Research Station, meteorological data from the Abisko Observatory; monthly sums for 1991–2018). Mean annual (covering years 1914–2013) precipitation in the area is 307 mm (Abisko Scientific Research Station). In 2018, the year of the latest vegetation survey and CO_2 measurements, the annual mean temperature was −0.2°C and the precipitation 287 mm. The mean temperature of July in 2018 was

15°C, the second warmest in the recorded history and around 1.5°C above the long-term average.

In the area, mountain birch (*Betula pubescens* ssp. *czerepanovii*, hereafter *B. czerepenovii*) forms the treeline. The forest understorey is dominated by the dwarf shrubs *E. hermaphroditum*, *Vaccinium myrtillus* and *Vaccinium uliginosum* and the grass *Deschampsia flexuosa*. Bryophytes are common, but only a few species of lichens are found (Kaarlejärvi et al., 2012). In tundra, the field layer is dominated by the dwarf shrubs *E. hermaphroditum*, *V. vitis-idaea*, *B. nana*, *V. uliginosum* and the bottom layer by lichens such as *Peltigera aphtosa* and *Nephroma arcticum* and bryophytes such as *Ptilidium ciliare* (Kaarlejärvi et al., 2012). In the area, the vegetation is affected by background herbivory as well as cyclic population outbreaks of insects and rodents (Callaghan et al., 2013; Kristensen et al., 2020; Olofsson et al., 2013). Several rodent and geometric moth outbreaks have occurred while the current experiment has been ongoing and some of them have caused severe damage to the vegetation. Most notable is the severe geometric moth outbreak by *Epirrita autumnata* and *Operophthera brumara* in 2012 (Olofsson et al., 2013).

The forest and tundra sites used in this study belong to a network of experiments established in mountain birch forests and tundra heath patches in 1998 (Sjögersten et al., 2003). By the time of the study site establishment, no permission for the fieldwork was required and the nature of the experiment does not contravene protections currently in place in the area. For this study, we included seven control plots (1 m²) and seven experimentally warmed plots, randomly set out at the mountain birch forest site, and eight control plots and eight warmed plots at the tundra site (Table 1). Warming was induced using International Tundra Experiment (ITEX) hexagonal

FIGURE 1 Location of the study area on the map and photos of two study sites: Tundra and Forest. Photo credit: Minna Männistö.

TABLE 1 Replication statement.

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Plots	Square or hexagonal field plot	7 or 8 of each combination, except 4 or 5 for comparison between years

OTCs with a maximum basal diameter of 146 cm. Vegetation in OTCs as well as in the control plots only includes species from the field and ground layers and no *B. czerepenovii* trees grow in the plots. At the early phases of the experiment, OTCs increased July air temperatures by 0.8 and 2.5°C in the forest and the tundra sites respectively (Sjögersten et al., 2003). No air temperature is available for the time of the present investigation, but the average soil temperature, measured every 2 h at 3 cm depth for 8 June–20 August 2018 using EasyLog EL-USB-1 data loggers (Lascar Electronics, Whiteparish) was 9.1 ± 0.4°C and 9.4 ± 0.2°C in the control and OTC plots in the forest site, and 8.7 ± 0.3 and 8.1 ± 0.5°C in the control and OTC plots in the tundra site respectively. Increased plant abundances insulated the ground to an extent that the OTCs experienced soil temperatures close to those in the control plots in the forest, and even lower temperatures than control plots in the tundra site (Stark et al., 2023).

2.2 | Vegetation analyses

The plant community composition was earlier recorded in 1999 and 2009 in five control plots and five OTCs in both habitats (Kaarlejärvi et al., 2012). We used the same plots during the present investigation and analysed the composition of vegetation in July 2018 with the point intercept method: in OTCs, a total of 87 pins was systematically distributed among three diagonals of the hexagons, 29 pins per diagonal (as in Kaarlejärvi in 2012). For each pin, the total number of hits as well as the height of the highest hit were recorded for each plant. Only one hit for each species was counted at the ground layer for each pin. The same method was applied to control plots. Later the total number of hits was normalized to hits per 100 pins. Data from one forest plot were discarded because of poor plot condition.

2.3 | Ecosystem carbon flux analyses

For the ecosystem carbon flux analyses, we included a few additional plots to have seven plots per treatment in the forest and eight plots per treatment in the tundra. The fluxes were analysed at 2-week intervals throughout the growing season 2018 (from 5 June to 19 August) using a closed system composed of a custom-built acrylic chamber (diameter 146 cm, height 60 cm) coupled to a Vaisala Carbon Dioxide Probe GMP343, Vaisala Humidity and Temperature Probe HMP75 and Vaisala Measurement Indicator MI70. Measurements included four consecutive measures of gradually changing light intensity: ambient light, 35% and 60% shading, and darkness to reveal ecosystem respiration, R_e. Shading was implemented using hoods made of single- and double-layer white mosquito nets while darkness was obtained by covering the chamber with an opaque white hood. The chamber was vented before each measurement and placed carefully on top of the study plot so that the leakage of air from beneath the chamber was minimized (as in Väisänen et al., 2014). Photosynthetically active radiation (PAR) within the chamber was recorded using an HD 9021 Quantum-Photo-Radiometer. The CO_2

concentration, temperature and humidity within chambers were logged at 5-s intervals for 90 s. The CO_2 flux was calculated using CO_2 and the chamber microclimate data and corrected for changes in temperature and water vapour pressure (Hooper et al., 2002). The net CO_2 flux with light intensity above zero was regarded as NEE. For NEE, negative fluxes indicate a net uptake of CO_2 from the atmosphere, whereas positive fluxes indicate a net release of CO_2 into the atmosphere.

For the comparison of daily CO_2 flux measurements between the treatments and control plots we normalized GPP to the PAR level of $600 \,\mu mol \, m^{-2} s^{-1}$. The GPP was calculated from the NEE and R_e as:

$$GPP = NEE - R_e. \tag{1}$$

Daily plot-specific GPP values were fitted to their corresponding PAR levels using the nonlinear least squares (nls) function from stats package in R software environment as (R Core Team, 2021):

$$GPP_{ij} = \frac{A_{max}PAR}{k + PAR}, \tag{2}$$

where i stands for ith plot and j for jth date, A_{max} is the maximum GPP rate when saturated to light $(mg \, CO_2 \, m^{-2} h^{-1})$ and k is the half-saturation light constant $(\mu mol \, m^{-2} s^{-1})$. Subsequently, the GPP_{600} was calculated for each plot and day at the light level of $600 \,\mu mol \, m^{-2} s^{-1}$ using Equation (2) with PAR set to 600 (Figure S1).

2.4 | Statistical analyses

To test the effects of OTC, habitat, time (year or date) and their interactions on the abundance of total vegetation, plant species and plant functional types, and on NEE_{600}, GPP_{600} and R_e, we used a repeated measures ANOVA. When ANOVA revealed a significant interaction, pairwise t-test was used to test the effect of year, habitat or OTC in the split data. The normality of data distribution was evaluated using the Shapiro–Wilk test and histograms, and the homogeneity of variances using the Levene's test. To meet the assumptions of ANOVA, *B. nana*, *V. uliginosum* and graminoid abundances were square root transformed. The abundance of *B. nana* and *V. myrtillus* were tested only for warming and year effects, since they grew almost exclusively in one of the habitats only. The abundances of forbs and pteridophytes were not tested individually as they grew only on few plots.

To investigate the links between CO_2 fluxes and total vascular plant, deciduous and evergreen shrub abundances, residual flux data devoid of habitat effect were first produced using ANOVA with habitat as a predictor. Pearson correlation was then used to test the significance of associations between plant abundances and residual CO_2 fluxes. If correlations were calculated with original data they would be dominated by mean habitat differences and would not reflect the within-habitat association of variables across study plots. Finally, the vascular vegetation from all plots, where the CO_2 exchange was measured, was fitted to an ordination diagram with non-metric multidimensional scaling using the vegan package

(Oksanen et al., 2022). All statistical analyses were performed and figures drawn with R software version 4.1.0 for statistical computing (R Core Team, 2021).

3 | RESULTS

3.1 | Vegetation development

We observed a significant treatment×habitat×year interaction effect on total vascular plant abundance (Table 2; Figure 2). A significant positive effect of OTCs was found in both forest ($p=0.006$) and tundra ($p=0.026$) in 2009 (with an especially strong effect in forest where vascular plants were 126% more abundant in OTCs than in controls), and a positive OTC effect was found in tundra ($p=0.003$) but not in forest ($p=0.101$) in 2018 (Figure 2). In control plots, the total abundance of vascular plants did not change significantly from 1999 to 2009 ($p=0.674$ in forest and $p=0.123$ in tundra) or from 2009 to 2018 ($p=0.704$ in forest and $p=0.164$ in tundra) (Figure 2). In contrast, the abundance increased by 118% in forest ($p=0.04$) and by 103% in tundra ($p<0.001$) (Figure 2) in OTCs from 1999 to 2009, with no further statistically significant changes in the abundance from 2009 to 2018 in either forest ($p=0.211$) or tundra ($p=0.724$). Overall, the vascular plants were 71% and 59% more abundant in OTCs than control plots in years 2009 and 2018 respectively.

Throughout the years, a major part of the vegetation consisted of dwarf shrubs, both deciduous and evergreen. The overall percentage of dwarf shrubs of the total vascular plant abundance was 79%, 95% and 90% in the years 1999, 2009 and 2018 respectively. In both habitats, evergreen dwarf shrubs dominated over deciduous ones. Evergreen dwarf shrubs were on average 51% more abundant in OTCs than controls in both 2009 ($p=0.006$) and 2018 ($p=0.002$), but not in 1999 ($p=0.436$) (Figure 3). The abundance increased on average by 133% from 1999 to 2009 ($p<0.001$), but then decreased by 30% from 2009 to 2018 ($p=0.003$). *Empetrum hermaphroditum* dominated the evergreen dwarf shrubs: on average, it formed 83% of the functional group abundance and 56% of the total vascular vegetation, but the abundance differed between the habitats (Table 2), being 143% higher in tundra than forest (Figure 3). Response of evergreen shrubs to warming was largely driven by *E. hermaphroditum* (Figure 3). Another evergreen dwarf shrub species, *V. vitis-idaea*, formed on average 15% of total abundance (see Figure S2 and Table S1 for *V. vitis-idaea* results).

The deciduous dwarf shrubs made up on average 22% of the total vascular vegetation. Their abundance was on average 72% higher in OTCs than controls (Table 2; Figure 3). There was a significant year×habitat effect (Table 2) because deciduous shrubs were 557% more abundant in forest than in tundra in 1999 ($p<0.001$), while no significant habitat effect was observed later in 2009 ($p=0.639$) and 2018 ($p=0.584$). Accordingly, the abundance of deciduous dwarf shrubs increased by 757% from 1999 to 2018 in tundra ($p=0.005$), but not in forest ($p=0.883$) (Figure 3). *Betula nana* grew almost exclusively in tundra, where it was on average 131% more abundant

TABLE 2 F- and p-statistics of ANOVA of the effects of treatment (control and OTC plots), year (1999, 2009 and 2018) and habitat (forest and tundra) on total vascular plant, functional group and species abundances.

	Treatment		Year		Habitat		Treatment×year		Treatment×habitat		Year×habitat		Treatment×habitat×year	
	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Vascular plants	25.027	**<0.001**	14.700	**<0.001**	21.158	**0.001**	5.791	**0.010**	0.074	0.788	2.228	0.133	6.301	**0.007**
Evergreens	11.048	**0.003**	17.876	**<0.001**	54.157	**<0.001**	4.809	**0.019**	0.915	0.350	3.095	0.066	2.617	0.097
E. hermaphroditum	8.270	**0.009**	13.068	**<0.001**	42.908	**<0.001**	3.400	0.053	0.479	0.496	1.546	0.236	2.226	0.133
Deciduous	19.156	**<0.001**	5.723	**0.010**	2.489	0.130	3.366	0.054	2.018	0.170	6.455	**0.007**	2.575	0.100
B. nana[a]	6.267	**0.021**	9.373	**0.001**	—	—	0.968	0.390	—	—	—	—	—	—
Graminoids[a]	1.202	0.285	6.921	**0.005**	25.767	**<0.001**	4.889	**0.018**	0.428	0.520	17.637	**<0.001**	0.240	0.789
Bryophytes	4.236	0.052	3.205	0.061	11.482	**0.003**	2.497	0.106	0.242	0.628	8.866	**0.002**	0.365	0.699

Note: Significance for $p \leq 0.05$ is indicated by bold.
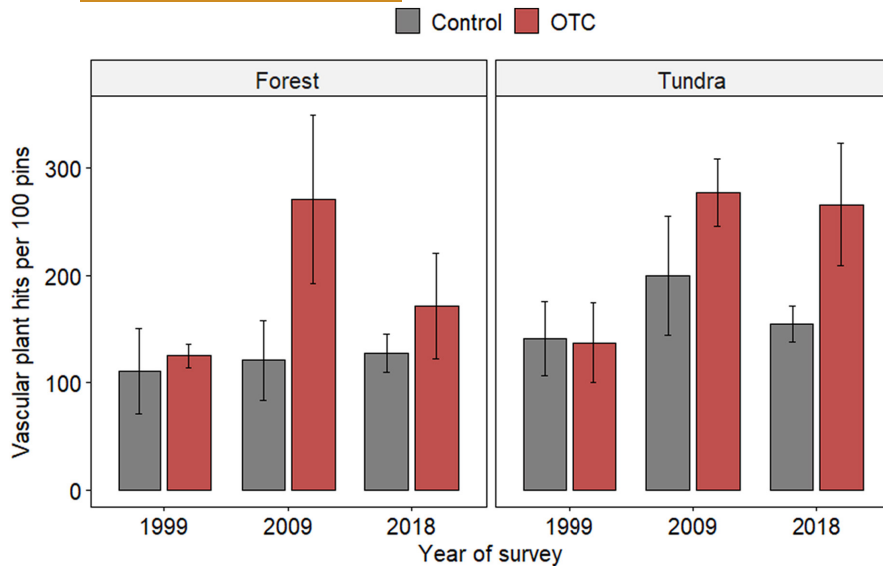[a]Square root transformed.

FIGURE 2 Vascular plant abundance (mean ± SD, $n = 4–5$) in control and OTC plots from 1999 to 2018 in forest and tundra habitats.

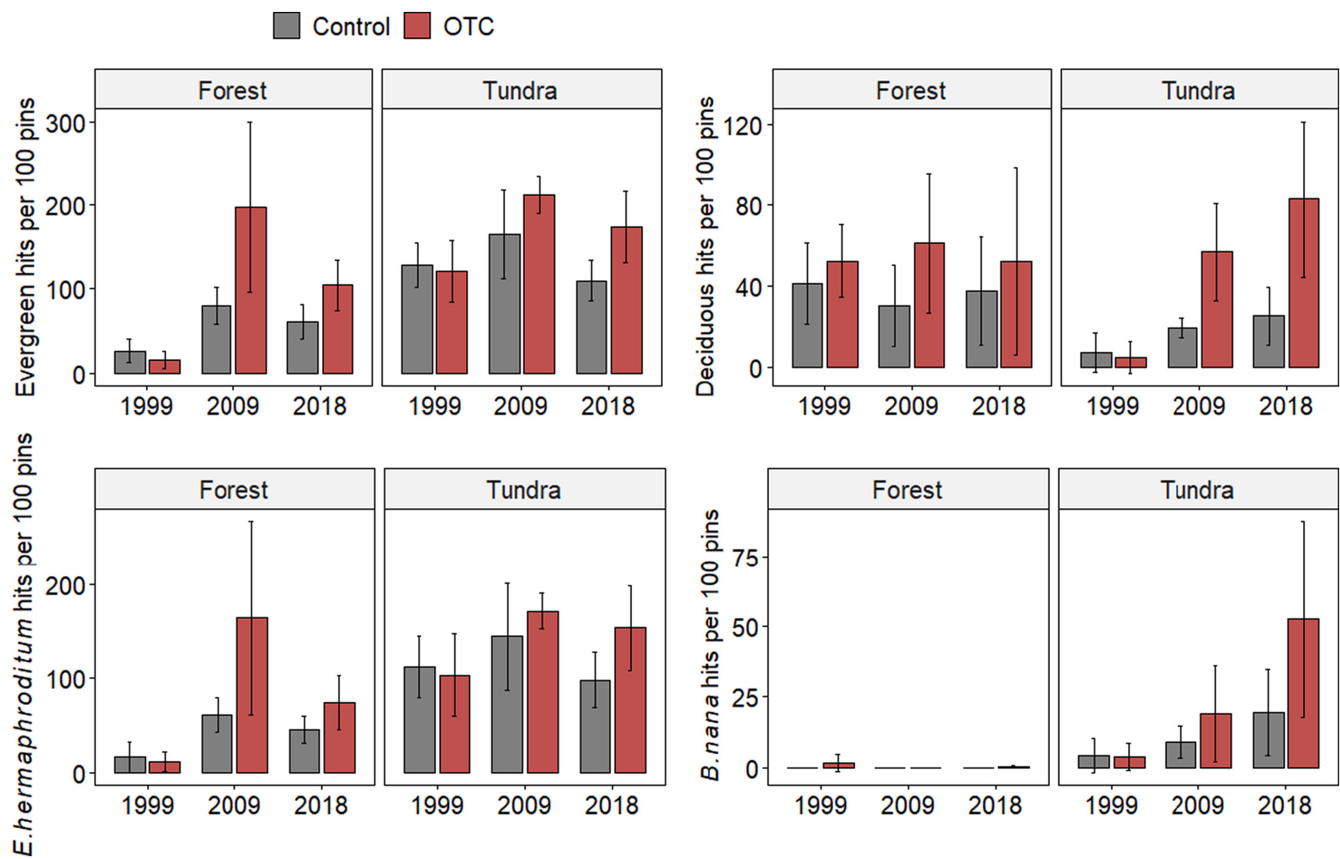**FIGURE 3** Abundance (mean ± SD, $n = 4–5$) of all evergreen and deciduous dwarf shrubs, *Empetrum hermaphroditum* and *Betula nana* in control and OTC plots from 1999 to 2018 in forest and tundra habitats.

in OTCs than controls (Table 2; Figure 3) and where its abundance increased through the years in both treatments, first by 258% from 1999 to 2009 ($p = 0.036$) and then further by 157% from 2009 to 2018 ($p = 0.002$) (Figure 3). The two other common deciduous dwarf shrub species were *V. myrtillus* and *V. uliginosum*. Of these, *V. uliginosum* was common in both habitats, while *V. myrtillus* grew almost

exclusively in forest (see Figure S2 and Table S1 for *V. myrtillus* and *V. uliginosum* results).

For graminoids the year×habitat interaction effect (Table 2) was due to graminoids being more abundant in forest than tundra in 1999 ($p < 0.001$), but not in 2009 ($p = 0.397$) or 2018 ($p = 0.335$) (Figure 4). Accordingly, their abundance decreased by 70% from
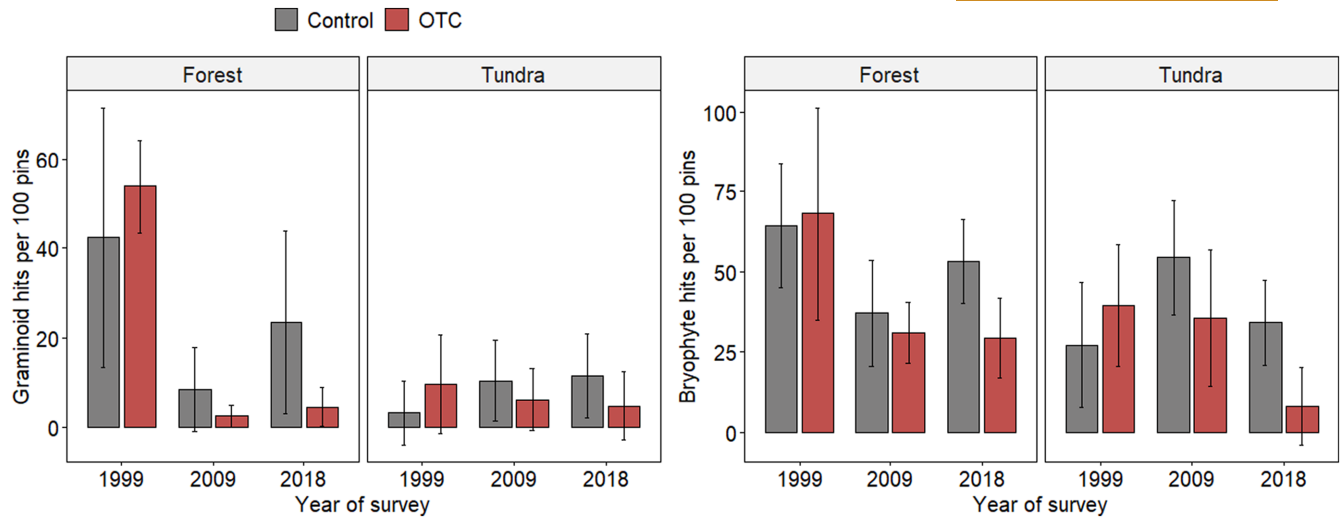
FIGURE 4 Abundance (mean ± SD, $n = 4$–5) of graminoids and bryophytes in control and OTC plots from 1999 to 2018 in forest and tundra habitats.

1999 to 2009 in forest ($p = {<}0.001$), but not in tundra ($p = 0.352$) (Figure 4). The year × treatment effect (Table 2) appeared because graminoids were significantly more abundant in controls than in OTCs in 2018 ($p = 0.049$), but not earlier. For bryophytes, the habitat × year interaction effect (Table 2) was because bryophytes were more abundant in forest than tundra in 1999 ($p = 0.005$) and 2018 ($p = 0.018$), but not in 2009 ($p = 0.2$). OTCs decreased bryophyte abundance on average by 24% (Figure 4), but this effect remained marginally significant (Table 2).

3.2 | CO_2 exchange

NEE_{600}, GPP_{600} and R_e varied across the growing season, and for all three variables the habitat and treatment effects depended on the measurement date (Table 3). The three-way treatment × habitat × date interaction was statistically significant for NEE_{600} (Table 3): no significant OTC effect was observed in tundra ($p = 0.122$), whereas in forest, OTCs increased NEE_{600} ($p < 0.001$) from mid-June to the end of July, but not in the first and last measurement (Figure 5a). Tundra acted as a C sink throughout the growing season and NEE_{600} remained relatively stable from July to August in both treatments (Figure 5a). In forest, NEE_{600} varied more in time and control plots shifted temporarily from sink to source in late July (Figure 5a). The mean growing season NEE_{600} was on average 64% more negative in OTCs than controls (Figure 5b; Table 4).

Treatment × habitat interaction effect on mean growing season GPP_{600} (Figure 5d; Table 4) was because OTCs increased GPP_{600} by 25% in forest ($p = 0.070$), while no statistically significant effect appeared in tundra ($p = 0.118$). A treatment × habitat × date interaction effect was also observed on GPP_{600} although the effect was only marginally significant (Table 3; Figure 5c). In tundra, GPP_{600} was on average 91% higher in control than OTCs in the fourth and sixth measurements ($p = 0.036$ and $p = 0.013$ respectively), while in forest,

GPP_{600} was 161% higher in OTCs than controls in the second measurement ($p = 0.029$) (Figure 5c).

The mean growing season R_e differed between habitats and treatments (Table 4): R_e was on average 28% greater in forest than tundra and on average 74% greater in controls than OTCs (Figure 5f). For R_e, the treatment × date interaction effect (Table 3) was because R_e was on average 48% lower in OTCs than controls in the last three measurements ($p = 0.001$, $p = 0.009$, $p < 0.001$ respectively), but not yet in June (Figure 5e). The habitat × date interaction effect appeared because R_e was similar or higher in tundra than forest until mid-July, but lower in tundra than forest in later measurements (Figure 5e).

3.3 | Correlations between plant group abundances and CO_2 fluxes

When the abundance of all vascular plants and evergreen and deciduous dwarf shrubs were contrasted with the residuals of CO_2 fluxes devoid of the habitat effect, the only statistically significant correlation that appeared was between residual R_e and total vascular plant abundance (Figure 6; Table 5). This correlation was negative, as was the marginally significant correlation between evergreen dwarf shrub abundance and residual NEE_{600} (Figure 6; Table 5).

3.4 | Multivariate analysis of treatment and habitat effects on vegetation

The non-metric multidimensional scale analysis (NMDS) of vascular plant abundances from 2018 clearly separated forest and tundra habitats (Figure 7). Within the habitats, the treatments overlapped but the treatment effect was still clear and OTCs from the two habitats resembled each other more than the controls did. Fitted vectors with a significant p-value show that both deciduous and evergreen

TABLE 3 F- and p-statistics of ANOVA of the effects of treatment (control and OTC plots), habitat (forest and tundra) and date (time of the growing season) on ecosystem NEE_{600}, GPP_{600} and R_e.

	Treatment		Habitat		Date		Treatment × habitat		Treatment × date		Habitat × date		Treatment × habitat × date	
	F	p	F	p	F	p	F	p	F	p	F	p	F	p
NEE_{600}	13.509	**<0.001**	0.362	0.549	5.284	**<0.001**	5.099	**0.027**	2.204	0.0630	7.754	**<0.001**	2.376	**0.047**
GPP_{600}	0.006	0.939	1.059	0.307	4.936	**<0.001**	6.408	**0.014**	3.437	**0.008**	2.759	**0.025**	2.099	0.075
R_e	33.281	**<0.001**	9.135	**0.003**	35.065	**<0.001**	1.904	0.172	5.411	**<0.001**	4.312	**0.002**	0.647	0.665

*Note:* Significance for $p \leq 0.05$ is indicated by bold.

dwarf shrubs increased towards tundra ($r^2 = 0.26$, $p = 0.009$ and $r^2 = 0.18$, $p = 0.049$ respectively), with the deciduous shrubs increasing especially towards OTCs. None of the CO_2 fluxes gained a statistically significant value and appeared in the NMDS diagram.

4 | DISCUSSION

The effects of warming on shrub abundance followed in many parts our predictions and earlier observations, whereas the effects on ecosystem CO_2 exchange contrasted our predictions. In particular, warming effects on R_e were negative, not positive, which calls for a reconsideration of mechanisms that link warming and CO_2 fluxes in northern ecosystems. We predicted that after 20 years, (H1) warming should have a stronger positive effect on dwarf shrub growth in tundra than forest because plant growth may be more sensitive to changes in temperature in tundra (Sundqvist et al., 2020), and an earlier survey had found increased abundance of *B. nana* (Kaarlejärvi et al., 2012). In line with our first hypothesis, OTCs had significantly higher total abundance of vascular plants than control plots in tundra, but not in forest in 2018 (Figure 2), and as expected, *B. nana* was driving this difference as other shrubs responded to warming similarly in both habitats (Figure 3). In particular, *E. hermaphroditum* abundance was higher in OTCs than controls in both habitats (Figure 3). Our prediction that (H2) OTCs will increase GPP and R_e in both habitats was clearly refuted: warming decreased R_e in both habitats and increased GPP only in forest (Figure 5f). These results also refuted our prediction that warming should increase R_e more in tundra than forest due to the positive effect of *B. nana* on carbon cycling, and that (H3) the greater increase in R_e under warming in tundra should outweigh the increase in GPP and result in reduced ecosystem C sink strength (i.e. a less negative NEE). In contrast, ecosystem C sink strength was significantly stronger in OTCs than controls in both habitats (Figure 5b). For forest, we predicted (H3) a neutral or slightly positive warming effect on C sink strength as warming was earlier shown to increase the abundances of evergreen dwarf shrubs in forest (Kaarlejärvi et al., 2012). This prediction was supported in terms that the positive effect of warming on C sink strength was stronger in forest than tundra (Figure 5a,b).

4.1 | Vegetation development

Our results add to the cumulating evidence that woody shrubs are driving the Arctic greening under climate warming through both increasing production and expanding distribution (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012): evergreen shrubs were on average 51% more abundant in OTCs than controls in the 2009 and 2018 surveys (Figure 3) and deciduous shrubs on average 72% more abundant in OTCs than controls (Figure 3). Shrub expansion has been associated with increasing abundance of deciduous species (e.g. Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012;
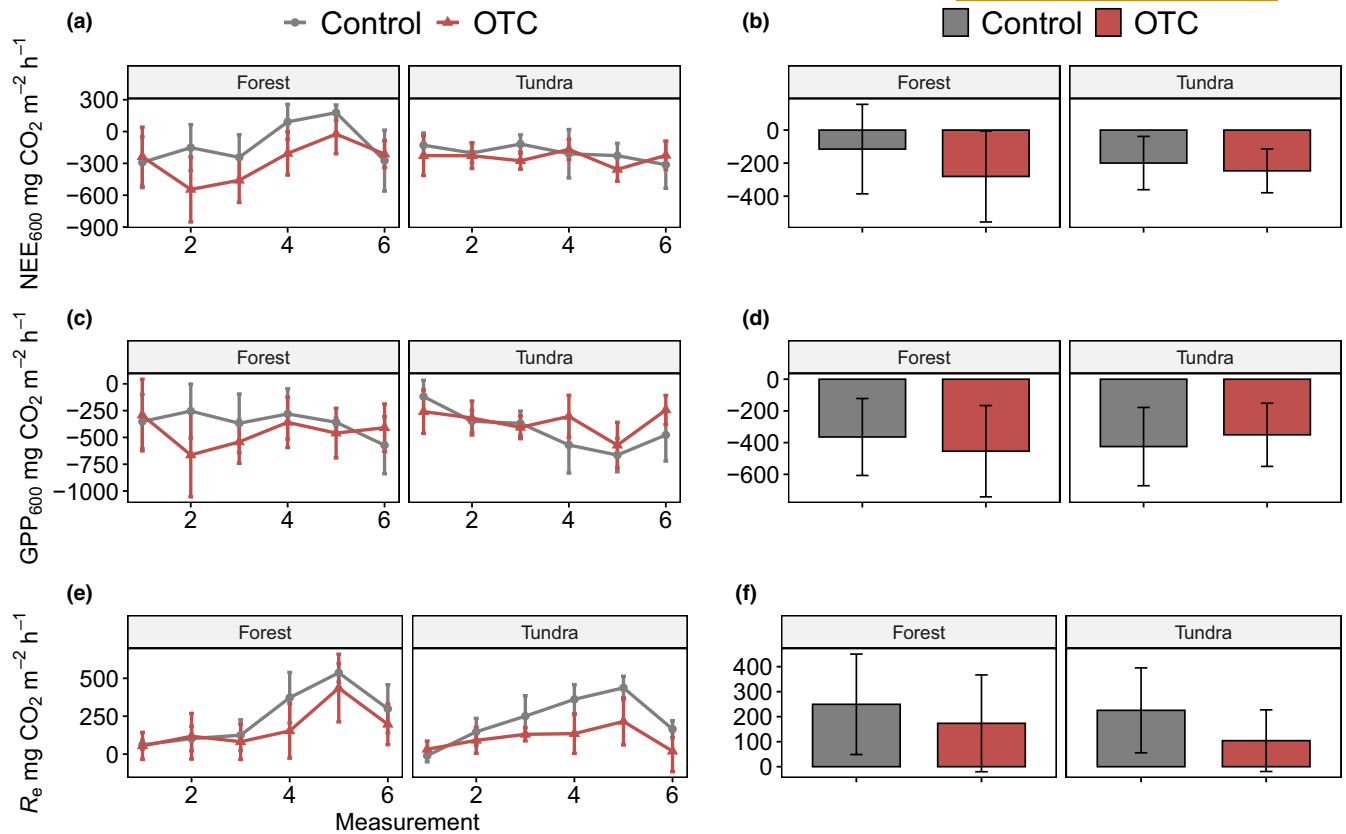
FIGURE 5 Measurement (a, c, e) and growing season (b, d, f) means (± SD) of NEE_{600}, GPP_{600} and R_e in forest and tundra habitats in 2018. All values are expressed as $mg\,CO_2\,m^{-2}\,h^{-1}$. Measurement 1 = 6–7 June, 2 = 17–19 June, 3 = 30 June–1 July, 4 = 13–16 July, 5 = 27–28 July and 6 = 18–19 August.

TABLE 4 F- and p-statistics of ANOVA of the effects of treatment (control and OTC plots) and habitat (forest and tundra) on growing season averages of ecosystem NEE_{600}, GPP_{600} and R_e.

	Treatment		Habitat		Treatment × habitat	
	F	p	F	p	F	p
NEE_{600}	10.323	**0.003**	0.626	0.436	3.454	0.074
GPP_{600}	0.005	0.946	0.375	0.546	5.417	**0.028**
R_e	26.702	**<0.001**	5.823	**0.023**	1.341	0.257

*Note*: Significance for $p ≤ 0.05$ is indicated by bold.

Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012; Myers-Smith et al., 2011), but recent studies have also found strong increases in the abundance of evergreen species (Stark et al., 2021; Vuorinen et al., 2017). In our study, both evergreen and deciduous shrubs increased under warming, but the greater percentual increase in deciduous than evergreen shrubs suggest that, also in our study area, the deciduous shrubs benefit of warming relatively more than the evergreen shrubs.

Supporting the idea that shrub expansion often occurs at the expense of graminoids (e.g. Myers-Smith et al., 2011) and bryophytes (Alatalo et al., 2020), we found that the abundances of graminoids and bryophytes were lower in OTCs than controls (Figure 4). Considering that graminoids are the plant group in Arctic environments whose growth most closely follows soil nutrient availability (Croll et al., 2005), the negative warming effect may be mediated

by the decelerated soil nutrient mineralization, supposedly following the accumulation of *E. hermaphroditum* litter (Bråthen et al., 2017; Vowles & Björk, 2018). Bryophytes in turn likely decrease when the dominant shrubs become so tall that they limit light availability at the ground layer (Alatalo et al., 2020).

Although the OTC effect on plant groups in our study largely followed our predictions, changes along the years show that the OTC effect was not cumulative. Most notably, only *B. nana* of all shrub species had higher abundance in OTCs in 2018 than in 2009. The likely reason for this finding is a series of herbivore outbreaks that took place in the study area between 2009 and 2018. The geometric moth outbreaks by *E. autumnata* and *O. brumata* in 2012 and 2013, a lemming outbreak in 2011 (Callaghan et al., 2013; Olofsson et al., 2013) and another moth outbreak in 2017 (S. Sjögersten, personal observation) had drastic effects
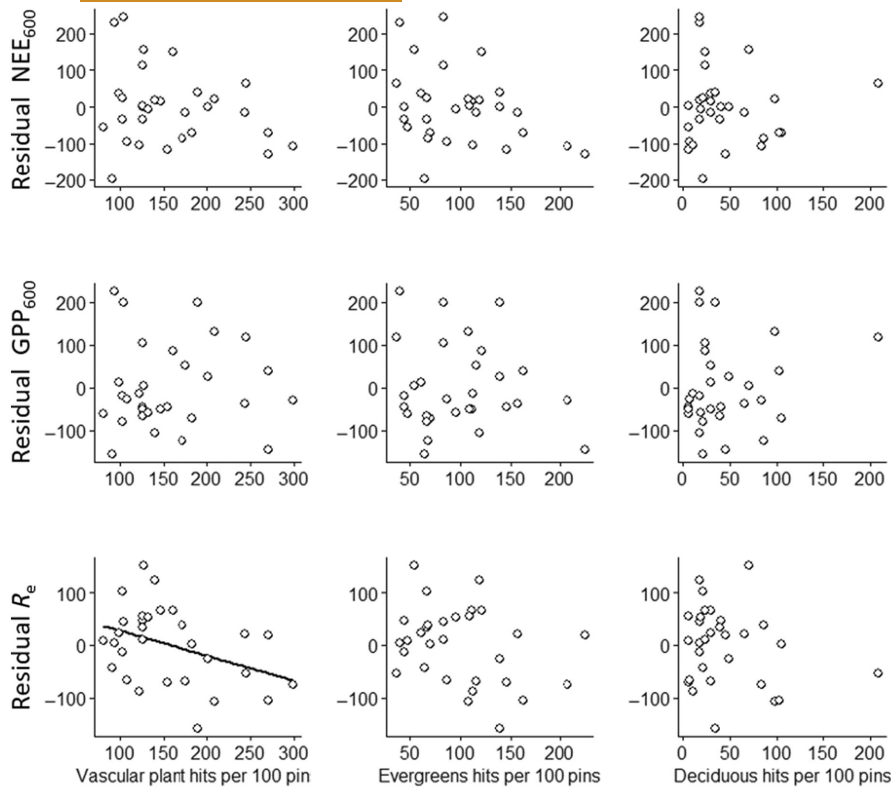
FIGURE 6 Association of the abundance of all vascular plants and evergreen and deciduous dwarf shrubs with CO_2 flux residuals devoid of habitat effect.

TABLE 5 Correlation coefficients and p-values of Person correlation between plant groups and CO_2 flux residuals devoid of habitat effect.

	Residual NEE$_{600}$		Residual GPP$_{600}$		Residual R_e	
	r	p	r	p	r	p
Vascular plants	−0.25	0.180	0.03	0.890	−0.39	**0.032**
Evergreens	−0.34	0.068	−0.12	0.520	−0.31	0.099
Deciduous	−0.01	0.950	0.14	0.450	−0.22	0.250

Note: Significance for p ≤ 0.05 is indicated by bold.

on the mountain birches and the ground vegetation, and a study at nearby plots reported 34%–76% reductions of biomass for dwarf shrub species after the outbreaks (Olofsson et al., 2013). Microtine rodents can significantly reduce the abundance dwarf shrubs, including the lower palatability species like *E. hermaphroditum* (Olofsson et al., 2014; Tuomi et al., 2019), as well as bryophytes (Olofsson et al., 2014). The rodent outbreak thus likely explains the decline in bryophytes in tundra between 2009 and 2018. Both moth and rodent outbreaks have regular cycles in subarctic Fennoscandia and can be seen as natural drivers of vegetation (Callaghan et al., 2013; Olofsson et al., 2013, 2014). Our results from a long-term experiment provide a novel perspective into how strongly these drivers can control vegetation trajectories under warming Arctic.

Assuming that herbivore outbreaks caused comparable damage to all shrub species in our study plots, *B. nana* appears as an exception in two ways. First, the positive OTC effect seemed to accumulate in *B. nana* abundance over years despite herbivory. Second, *B. nana* abundance also increased in tundra controls over years, thus suggesting that, despite herbivory outbreaks, *B. nana* could also benefit of the naturally increasing temperatures over the study period

(Rantanen et al., 2022). These results are in line with the high plasticity of *B. nana* growth strategy (Bret-Harte et al., 2001). Altogether our results support the framework that herbivory outbreaks may nullify the cumulation of positive warming effects on plant growth (Kaarlejärvi et al., 2015), and further highlight that herbivory may promote species such as *B. nana* that both significantly benefit of warming and can quickly recover from damage.

4.2 | Growing season CO_2 exchange

While the vegetation mostly responded to warming as predicted, this was not the case for CO_2 exchange: instead, in contrast to several earlier warming experiments, which report increasing R_e under warming (Biasi et al., 2008; Oberbauer et al., 2007; Väisänen et al., 2014; Ylänne et al., 2015), we observed a clear decrease in R_e in both forest and tundra. This finding not only opposed our prediction, but also showed that the consequence of warming on R_e did not depend on whether deciduous or evergreen dwarf shrubs increase in abundance under warming, as suggested by Vowles and Björk (2018). We further predicted that warming will increase the

FIGURE 7 Two-dimensional non-metric multidimensional scale (NMDS) ordination of plant species composition within different treatments in 2018 (stress=0.17). The ordination shows the vectors of species and functional groups with a *p*-value less than 0.05. Ellipses represent 95% confidence intervals for treatment groups.
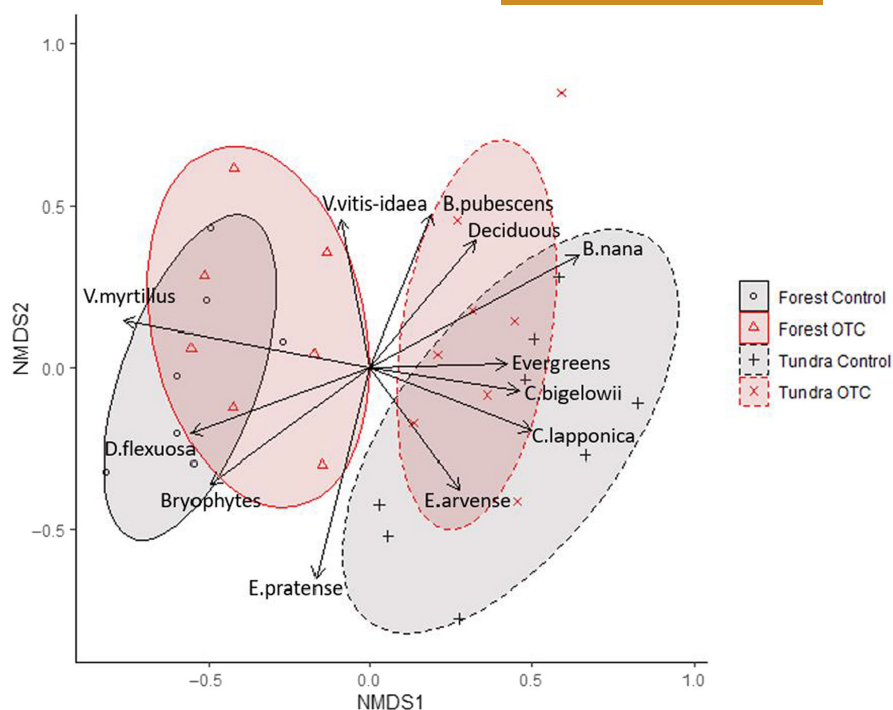
GPP in both habitats, but found a marginal positive effect only in forest. The effect of warming on the GPP was strongest during early growing season, a time period where light availability for the understorey vegetation is not yet limited by the tree leaves (Ťupek et al., 2008). Studies in the Arctic have indicated that the effect of warming on R_e rather than on GPP drives the pattern in NEE (Cahoon et al., 2012; Väisänen et al., 2014). In our study, both lower R_e and higher GPP contributed to increased C sink strength in forest, whereas in tundra, where no warming effect on GPP was detected, the lower R_e was the sole driver.

Our findings that GPP was not affected and R_e decreased under warming in tundra contrast earlier studies, which have suggested that increase in deciduous dwarf shrubs accelerates carbon cycling (Parker et al., 2021; Vowles & Björk, 2018) and that *B. nana* has a key role in this process even in sites where it accounts for a minor proportion of the total above-ground vascular plant biomass (Cahoon et al., 2016; Metcalfe & Olofsson, 2015). Although our result was unexpected, a number of studies have also found CO_2 fluxes in tundra to be relatively unresponsive to changes in plant community composition (Sundqvist et al., 2020; Ylänne et al., 2015). It therefore seems likely that under some conditions, other mechanisms outweigh the importance of plant species on ecosystem CO_2 exchange.

Noteworthy, we found a significant negative correlation between R_e and the total vascular plant abundance, indicating that the increase in total amount of vascular plants rather than a change in a single plant functional group was responsible for the lower R_e in OTCs. Previous studies have demonstrated that taller and denser vegetation cover buffers the soil against warmer air temperatures (e.g. Way & Lapalme, 2021; Weintraub & Schimel, 2005), and that the effect of shrubs on CO_2 exchange in tundra ecosystems depends on soil temperatures (Cahoon et al., 2012). Increased insulation of

soil through increased vascular plant cover could thus significantly contribute to the lower R_e under warming. Why this outcome has not been observed in other studies may derive from the longevity of our experiment: it may take decades until shrubs increase to the extent that their cooling impact on the growing season soil microclimate outweighs the direct effects of plant groups on CO_2 exchange. However, not even in our case can the indirect effects through soil microclimate solely explain decreasing R_e as we detected lower mean soil temperature and daily temperature maximums inside the OTCs in tundra, but not in the forest (Stark et al., 2023). In the forest, shading by *B. czerepanovii* trees likely diminishes the role of ground vegetation in soil microclimate. Results from the same experiment also suggest that nutrient competition between plants and soil microorganisms increase under warming, thus negating the effects of warming on microbial activity in C decomposition (Stark et al., 2023). It appears that several different mechanisms could contribute to decreasing R_e.

The growing season 2018 was especially hot and dry during the mid and late growing season. This led to a decrease in GPP and R_e in other parts of Fennoscandia (Silfver et al., 2020), but we found an increasing trend of GPP during the same phase of the growing season. We also found the highest R_e rates in mid and late July, suggesting that R_e followed the same pattern as temperature and was not negatively affected by high temperatures. These contrasts likely arise from differences in climate and other environmental factors between the research sites. The Silfver et al. (2020) study site in northern Finland has subcontinental climate, acidic bedrock and lower vegetation cover while our site has a more maritime climate with higher precipitation, more nutrient-rich bedrock and a thicker moss and dwarf shrub cover, which all likely buffer against severe moisture stress.

4.3 | Implications

Our findings of higher shrub abundances after 20 years of warming agree with the notion of Arctic shrubification (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012; Myers-Smith et al., 2020). However, owing to several population outbreaks of geometric moths and rodents during the experiment (Callaghan et al., 2013; Olofsson et al., 2013), the effect of warming on shrubs was not cumulative over time. The only exception was *B. nana*, which continued to increase in abundance over time in both controls and OTCs. Given that moth outbreaks will likely increase in frequency under warming climate (Jepsen et al., 2013), we suggest that climate warming may promote species that can combine efficient compensatory growth with a capacity of benefiting from improved growing conditions. Furthermore, in the long term, the indirect impact of increased total vascular plant abundance on soil microclimate may become increasingly important for ecosystem CO_2 exchange. Given the slow responses of dwarf shrub vegetation to changing temperatures and the cyclicity of herbivore outbreaks in the Arctic, only long-term field studies may be able to reveal the impact of climate warming on the dynamics of vegetation and the ecosystem C sink strength.

AUTHOR CONTRIBUTIONS

Sofie Sjögersten and Johan Olofsson established and maintained the field experiment. Sari Stark and Minna K. Männistö planned the present study with input from Johan Olofsson. Eero Myrsky performed new data collection. Eero Myrsky conducted statistical analyses together with Juha Mikola. Elina Kaarlejärvi, Johan Olofsson and Sofie Sjögersten contributed with earlier data. Boris Tupek processed the light standardization of the CO_2 exchange data. Eero Myrsky led the writing of the paper to which all co-authors contributed with discussion and text and gave the final approval of the paper.

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CONFLICT OF INTEREST STATEMENT

The authors state that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository (Myrsky et al., 2023): https://doi.org/10.5061/dryad.612jm649d.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Comparison between the observed and modelled GPP (mg CO_2 m^{-2} h^{-1}) and NEE (mg CO_2 m^{-2} h^{-1}) for control (a, d), tundra (b, e), and forest ground vegetation (c, f) study plots.

Figure S2: The significant year × habitat interaction effect on *V. vitis-idaea* abundance (Table S1) was because *V. vitis-idaea* was 231% more abundant in tundra than forest in 1999 ($p=0.021$) and 59 % more abundant in forest than tundra in 2018 ($p=0.021$), while no significant difference was found in 2009 ($p=0.516$).

Table S1: *F*-and *p*-statistics of ANOVA of the effects of treatment (control and OTC plots), year (1999, 2009 and 2018) and habitat (forest and tundra) on total vascular plant, functional group and species abundances.