



Plant co-occurrence patterns and soil environments associated with three dominant plants in the Arctic

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Background: The positive effects of Arctic plants on the soil environment and plant-species co-occurrence patterns are known to be particularly important in physically harsh environments. Although three dominant plants (*Cassiope tetragona*, *Dryas octopetala*, and *Silene acaulis*) are abundant in the Arctic ecosystem at Ny-Ålesund, Svalbard, few studies have examined their occurrence patterns with other species and their buffering effect on soil-temperature and soil-moisture fluctuation. To quantify the plant-species co-occurrence patterns and their positive effects on soil environments, I surveyed the vegetation cover, analyzed the soil-chemical properties (total carbon, total nitrogen, pH, and soil organic matter) from 101 open plots, and measured the daily soil-temperature and soil-moisture content under three dominant plant patches and bare soil.

Results: The *Cassiope tetragona* and *Dryas octopetala* communities increased the soil-temperature stability; however, the three dominant plant communities did not significantly affect the soil-moisture stability. Non-metric multidimensional scaling separated the sampling sites into three groups based on the different vegetation compositions. The three dominant plants occurred randomly with other species; however, the vegetation composition of two positive co-occurring species pairs (*Oxyria digyna*-*Cerastium arcticum* and *Luzula confusa*-*Salix polaris*) was examined. The plant species richness did not significantly differ in the three plant communities.

Conclusions: The three plant communities showed distinctive vegetation compositions; however, the three dominant plants were randomly and widely distributed throughout the study sites. Although the facilitative effects of the three Arctic plants on increases in the soil-moisture fluctuation and richness were not quantified, this research enables a deeper understanding of plant co-occurrence patterns in Arctic ecosystems and thereby contributes to predicting the shift in vegetation composition and coexistence in response to climate warming. This research highlights the need to better understand plant-plant interactions within tundra communities.

Keywords: Arctic ecosystem, *Cassiope tetragona*, *Dryas octopetala*, Ny-Ålesund, *Silene acaulis*, Soil temperature stability

Introduction

Alpine, sub-Arctic, and Arctic ecosystems are well known for their harsh and stressful environmental conditions, characterized by low temperatures, strong winds, and desiccation (Klanderud and Totland 2004). In the high Arctic, Ny-Ålesund of Svalbard (lying at 78° 55' N, 11° 56' E) is the world's northernmost settlement and, given its location, is an area of special environmental interest (i.e., bare soil, stones, crusts, mosses, and vegetation) (Chae et al. 2016; Dowdall et al. 2004). Svalbard is one of the places in the high Arctic where rapid changes in landscape forms have

occurred due to deglaciation, early snowmelt, enhanced growing season length, and drying of shallow ponds, all of which have resulted from climate warming (Kwon et al. 2015; Mallik et al. 2011; Thomas et al. 2020). Contrarily, some research argue that rises in winter temperatures and increases in winter precipitation (snowfall) and snow depth may lead to shorter growing seasons (Buus-Hinkler et al. 2006; Cooper et al. 2011; Mallik et al. 2011). Obviously, vegetation productivity in Arctic ecosystems has increased over the past few decades, resulting in a trend of greening that coincides with increases in the air temperature (which has climbed about 2°C per decade over the last 30 years)



(Pearson et al. 2013; Tape et al. 2006). Similarly, the increase in the growth and abundance of tundra shrubs has been expected in the circumpolar region over the last half-century (Angers-Blondin et al. 2018; Myers-Smith et al. 2015).

The plant species distribution and community characteristics are influenced by both biotic interactions and abiotic conditions, where the relative importance of each can depend on the spatial scale and environmental conditions (Bruno et al. 2003; Gouws et al. 2021). Arctic plant communities are determined by large-scale climatic variations or by local environmental conditions (Nabe-Nielsen et al. 2017). However, from early studies of plant community ecology, there have been debating views concerning the processes that assemble plant communities (Götzenberger et al. 2012). A biological community may contain either a random set of species or be structured by certain assembly rules (positive or negative relationship) (Vinarski et al. 2020). Plant-plant interactions in communities strongly affect the community structure and dynamics and can thereby determine which species can coexist (Padilla and Pugnaire 2006). Such interactions can be positive (facilitative), negative (competitive), or neutral (Lu et al. 2018). Facilitation and competition often co-occur in plant communities and are difficult to understand separately (Callaway and Walker 1997; Río et al. 2014). Besides, plant-plant interactions are driven by environmental conditions, functional traits, and evolutionary relatedness among interacting species, all of which are strongly related to each other (Soliveres et al. 2014; Webb et al. 2002).

According to the stress-gradient hypothesis, positive interactions are expected to be more frequent and more intense in more severe habitats (alpine, Arctic, Antarctic, and arid regions) (Bonanomi et al. 2016; Haussmann et al. 2010; Hupp et al. 2017; Pueyo et al. 2016; Soliveres and Maestre 2014), resulting in a stronger impact on individual species and communities in stressful environments (Gouws et al. 2021; He et al. 2013). An important type of positive plant interaction arises from nurse plants (e.g., *Silene acaulis*), which facilitate the growth and development of other plant species, typically by creating benign microhabitats (Antonsson et al. 2009).

Several studies on the plant ecology in Ny-Ålesund have examined vegetation development (Yoshitake et al. 2011), the photosynthetic characteristics of dominant plant species (Muraoka et al. 2008), colonization characteristics of *Salix polaris* (Nakatsubo et al. 2010), root-associated fungal communities among plant species (Davey et al. 2015), cover change of vegetation and glaciers (Ren et al. 2021), vegetation maps (Moreau et al. 2005), and relationships between snowmelt and plant distribution (Park et al. 2018); however, the vegetation composition and co-occurrence associated with the main dominant plant species have received much less attention. Moreover, the dominant plant

patches in Arctic environments remain poorly explored. Because plant communities in the high Arctic have shown strong responses to experimental and observed warming, identifying plant communities that are resistant to climate change will be critical for predicting accurate and wide-scale vegetation change (Hudson and Henry, 2010). In addition, Pearson et al. (2013) predicted that at least half of the vegetated areas will shift to a different physiognomic class and woody cover will increase by as much as 52%, resulting in positive feedback to greater climate warming. Such extensive changes to Arctic vegetation will have implications for climate, wildlife, and ecosystem services.

Despite the importance of Arctic vegetation for biodiversity and conservation in the tundra biome against climate warming, few attempts have been made to compare the vegetation composition including dominant plants and their positive effect on the soil-environment in the high Arctic (Grau et al. 2014). To recognize the changes in Arctic plant composition for climate change adaptation, it is crucial to describe the co-occurrence patterns of Arctic plants and their diversity, which are centered on three dominant plants (*Cassiope tetragona*, *Dryas octopetala*, and *Silene acaulis*). In addition, this study explicitly addresses the positive effects of three dominant plants on the abiotic soil environment and the differences in plant-species richness in the Arctic. I hypothesize that the three dominant plants buffer the daily variation of soil-temperature and soil-moisture and show the different patterns in plant-species co-occurrence, soil-chemical properties, and plant richness. The specific objectives of this study are (1) to quantify the daily differences in soil-temperature and soil-moisture among three dominant plants, (2) to verify the different vegetation compositions depending on the three dominant plants, (3) to describe the soil-chemical properties associated with three dominant plants, and (4) to reveal the co-occurrence pattern of three dominant plant species with other plant species and plant species richness.

Materials and Methods

Study area

The data were collected in July 2015 in Ny-Ålesund (78°55' N, 11°55' E) on Spitsbergen, the largest island of the Svalbard archipelago. This area was deglaciated ca. 11,000–13,000 years ago (Cannone et al. 2004), and mature vegetation is dominant in a portion of the study area (Park et al. 2018). The mean temperature is −3.2°C, and the average total annual precipitation of rain or snow was 490.5 mm for the period from 2011 to 2015 (Son and Lee 2022). For July 2015, the mean temperature and total precipitation equaled 6.6°C (maximum 14.8°C and minimum 2.3°C) and 13.2 mm, respectively (<https://www.yr.no>). Each year, the snow-

free period lasts from June to August; at other times during the year, the study area is snow-covered (Blaud et al. 2015). The vegetation's growing season only lasts from June to September each year due to the high latitude of Svalbard, and vigorous growth occurs only in July and August (Ren et al. 2021).

Study species

The vegetation in the study site was dominated by *Cassiope tetragona* (L.) D. Don, *Dryas octopetala* L., and *Silene acaulis* (L.) Jacq., while other abundant species were *Salix polaris*, *Luzula confusa*, *Saxifraga oppositifolia*, and *Bistorta vivipara*.

Cassiope tetragona (family: Ericaceae, Arctic bell-heather or white Arctic Mountain heather, hereafter *Cassiope* or *C.te*) and *D. octopetala* (family: Rosaceae, eightpetal mountain-avens or white dryad, hereafter *Dryas* or *D.oc*) are evergreen dwarf shrubs found throughout the Arctic, forming dense, compressed mats with a high-percentage of cover (Cooper and Wookey 2003; Son and Lee 2022; Weijers et al. 2017). *Silene acaulis* (family: Caryophyllaceae, moss campion or cushion pink, hereafter *Silene* or *S.ac*) is an alpine cushion plant and evergreen perennial (Antonsen et al. 2009).

Sampling design

The vegetation composition at a total of 101 sampling sites (area: about 220 m × 320 m) (Fig. 1) was investigated during July 2015. At each sampling site, I randomly placed a 1 m × 1 m quadrat at least 10 m away from the other quadrats to visually estimate species cover (%). Seventeen bare-soil quadrats without vascular plants were also included as a control. While simultaneously considering cover and frequency, the plots of the sampling sites named after the most abundant plant species with highest cover in each quadrat were divided into three groups: *Cassiope* (n = 29), *Dryas* (n = 20), and *Silene* (n = 35). I also recorded the patch area and patch height of a total of 416 patches (116 *Cassiope*, 94 *Dryas*, and 206 *Silene* patches) of three Arctic

plants using a ruler to examine the plant characteristics. The patch area was calculated by multiplying the length by the width. The species nomenclature I used for this study follows that of The Flora of Svalbard (<https://www.svalbardflora.no/>). The positions of all quadrats were recorded using a GPS device (Montana 610; Garmin, Cary, NC, USA).

To monitor the soil-environmental conditions, soil-temperature and soil-moisture were measured at intervals of 1 hour from 12 July 2015 to 18 July 2015 (5TM sensor; Decagon Devices Inc., Pullman, WA, USA) (Tables S1 and S2). For recording the soil-temperature, two measurement devices, each comprising four probes, were located 25 m apart. In each measurement group, the four probes were placed at a depth of 5 cm beneath the three plant species *Cassiope*, *Dryas*, and *Silene*, and in the bare soil. For recording the soil-moisture, only one measurement device worked, therefore, the soil-moisture data amount (seven samples per group, 28 total) is only half that of the soil-temperature data (14 samples per group, 56 total).

Simultaneously with the vegetation survey, I collected soil samples beneath the three plants or from the bare soil at each of the 101 sampling sites to quantify the local soil-chemical properties. Soil was taken from three locations per sampling site using a soil auger (corer dimensions: 5 cm diameter and 5 cm depth). Separately for each sampling site, the collected soil was mixed thoroughly to produce a composite sample. Soil analysis included the quantification of total carbon and total nitrogen using an element analyzer (EA1110; CE Instruments, Wigan, England) at the National Instrumentation Center for Environmental Management of Seoul National University. The soil EC and pH were measured with a glass electrode in an 1:5 soil-to-distilled-water slurry (Eutech PC 2700; EUTECH Instrument, Singapore). The soil organic matter was determined by measuring the amount of weight lost after drying the samples in a furnace at 550°C for 4 hours (Achat et al. 2012).

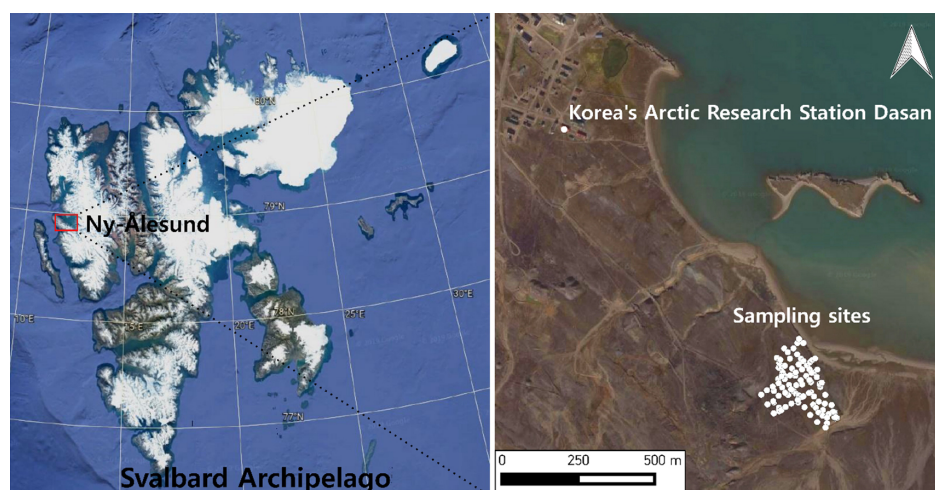


Fig. 1 Location of the 101 sampling sites in Ny-Ålesund (78°55' N, 11°55' E), Spitsbergen, near Korea's Arctic Research Station Dasan operated by the Korea Polar Research Institute.

Data analysis

Statistical analyses were performed using the R software (R Core Team 2022). First, species-cover values were log-transformed ($\ln[\text{cover} + 1]$) to reduce the influence of outliers. The significance of the distinctiveness in the vegetation composition between the three dominant plants was tested using the “adonis” function in the ‘vegan’ R package (Oksanen et al. 2018) to perform a permutation test with the F statistic (McGranahan et al. 2013). To describe the relationships between soil-chemical properties and plant-community compositions, I performed a NMDS based on the Bray-Curtis dissimilarities (species cover data) using the ‘metaMDS’ function of the ‘vegan’ R package (Oksanen et al. 2020). The environmental factors were fit a posteriori to the NMDS ordination, with the significant factors ($p < 0.05$) plotted as vectors. The species with an importance value ($[\text{relative cover} + \text{relative frequency}] / 2$) less than 1% were excluded in the NMDS analysis.

Second, to compare the buffering effect on daily soil-temperature differences and daily soil-moisture differences related to the three dominant plants, I used a Kruskal-Wallis test with Bonferroni correction due to the unequal n in each group (Curran et al. 2010; Le Gall et al. 2020). Soil-temperature differences and daily soil-moisture differences were calculated as the highest minus the lowest value during a day. To clarify the analysis of variance assumptions of independence, normality and homogeneity of variance, the variables were preliminarily checked (Zuur et al. 2010). Likewise, I compared the soil-chemical properties (i.e., total carbon [C], total nitrogen [N], electrical conductivity [EC], and soil organic matter [SOM]) among the three Arctic plant types as well as their patch areas and heights using a parametric unbalanced one-way analysis of variance (ANOVA) with Welch’s F ratio because the variances were not homogeneous (McDonald 2009; Tibbett et al. 2019). The significance of differences ($p < 0.05$) between the means of the three communities and bare soil were as-

sessed using Games–Howell honest significant difference (HSD) for post hoc comparisons (Le Gall et al. 2020). All analyses were carried out in the R environment for statistical computing and visualization (R Core Team 2022).

Third, the plant co-occurrence frequency was analyzed using the presence/absence data of the plant pairwise and “coocur” package in R software (Griffith et al. 2016) to detect positive and negative co-occurrences between species. This package employs a probabilistic approach to determine which species pairs co-occur less often (negative co-occurrence) or more often (positive co-occurrence) than is likely by chance (Brazeau and Schamp 2019).

Results

In total, 17 plant species from 10 families were found (Table S3) at the three dominant plant communities (29 *Cassiope*, 20 *Dryas*, and 35 *Silene* communities) at the sampling sites. Besides the three Arctic plants *Cassiope*, *Dryas*, and *Silene*, the five most abundant species were *Salix polaris* (82/84 plots), *Luzula confusa* (81/84 plots), *Saxifraga oppositifolia* (60/84 plots), *Bistorta vivipara* (43/84 plots), and *Oxyria digyna* (29/84 plots).

Daily soil-temperature and soil-moisture differences associated with three dominant plants

The two plants significantly reduced the daily soil-temperature fluctuations. This effect was especially pronounced for *Cassiope* and *Dryas* ($p < 0.05$), which showed less daily soil-temperature differences (maximum – minimum). Daily soil-temperature fluctuations were more stable beneath *Cassiope* than beneath *Dryas*, *Silene*, or in bare soil. This was evidenced by the fact that the difference in the daily soil-temperatures beneath *Cassiope* was the smallest (Fig. 2A): *Cassiope* ($2.9 \pm 0.2^\circ\text{C}$, mean $\pm$ standard

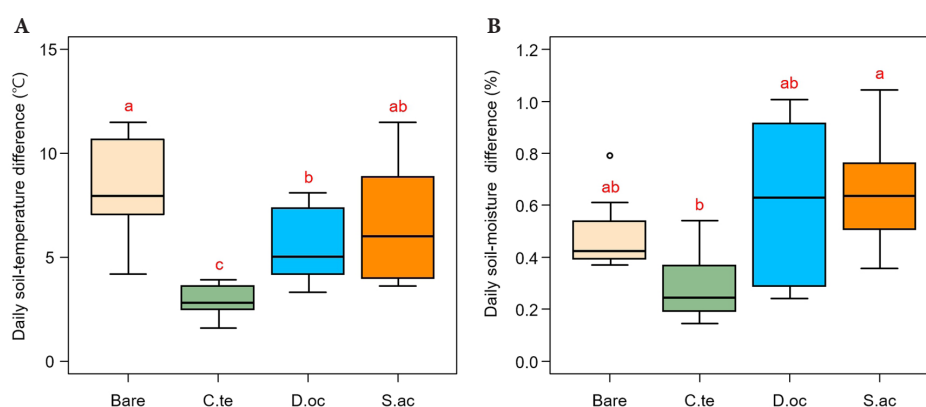


Fig. 2 Boxplots depicting the (A) daily soil-temperature difference in four groups (each $n = 14$) and (B) daily soil-moisture difference in four groups (each $n = 7$). Different letters (superscript a, b, and c) mean statistical differences ($p < 0.05$), as determined by a Kruskal-Wallis test with Bonferroni correction. The central horizontal lines within the boxes indicate the medians; box edges indicate the quartiles; whiskers indicate the minimum and maximum values; and the open circle indicates the outlier. Bare: bare soil; C.te: *Cassiope tetragona*; D.oc: *Dryas octopetala*; S.ac: *Silene acaulis*.

error [SE]) < *Dryas* ($5.7 \pm 0.5^{\circ}\text{C}$) < *Silene* ($6.6 \pm 0.7^{\circ}\text{C}$) < bare soil ($8.4 \pm 0.6^{\circ}\text{C}$). The difference in the daily soil-temperature in the presence of *Silene* was not significantly small compared to that of bare soil.

The three dominant plants did not significantly stabilize the soil-moisture differences (Fig. 2B). Even though *Cassiope* tended to reduce the daily soil-moisture fluctuations compared to *Silene*, there was no statistically significant soil-moisture difference between bare soil and the three plants. Therefore, the three dominant plants did not appear to have effects on soil-moisture stability.

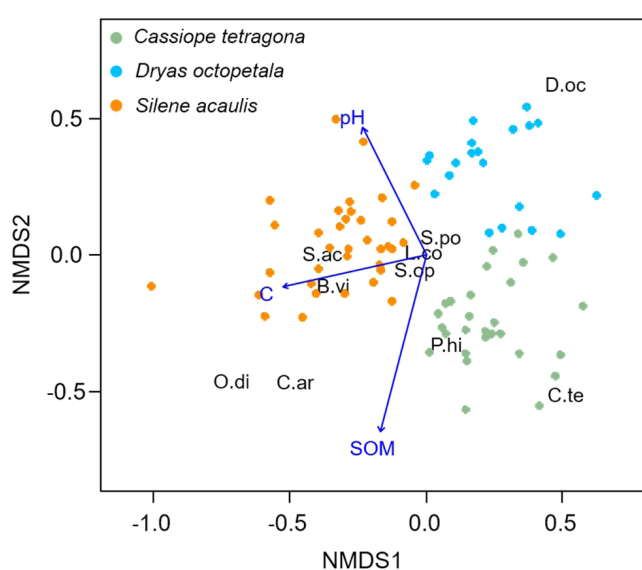


Fig. 3 Non-metric multidimensional scaling (NMDS) based on a similarity. The Bray-Curtis coefficient indicates a distinctive vegetation composition and relationships between species cover and soil-chemical properties. Seven species with less than 1% of the importance value were excluded in the NMDS analysis. Blue colored arrows indicate the significant variables ($p < 0.05$). The stress value of the NMDS is 0.19. Olive green circle, *Cassiope tetragona* plot; Sky blue circle, *Dryas octopetala* plot; Orange circle, *Silene acaulis* plot. C: total carbon; SOM: soil organic matter. B.vi: *Bistorta vivipara*; C.ar: *Cerastium arcticum*; C.te: *Cassiope tetragona*; D.oc: *Dryas octopetala*; L.co: *Luzula confusa*; O.di: *Oxyria digyna*; P.hi: *Pedicularis hirsuta*; S.ac: *Silene acaulis*; S.op: *Saxifraga oppositifolia*; S.po: *Salix polaris*.

Vegetation composition and soil-chemical properties

There was a significant distinctiveness in the vegetation composition between the three dominant plant communities that explained 48.9% of the compositional variance ($F = 38.8$; $p = 0.001$). The NMDS ordination (stress value: 0.19) also clearly showed the distinctiveness between the three dominant plant communities (Fig. 3). *Cassiope* communities are located at the positive end of axis 1 and the negative side of axis 2, while *Dryas* communities are placed at the positive sides of axis 1 and 2. In contrast, *Silene* communities are located at the negative end of axis 1 and both positive and negative sides of axis 2. Of the 10 most abundant species, *Bistorta vivipara* and *S. acaulis* were highly correlated with NMDS axis 1, while *C. tetragona*, *D. octopetala*, *Oxyria digyna*, and *Cerastium arcticum* were significantly correlated with NMDS axis 2.

The vegetation composition was significantly correlated with the following soil-environmental variables: total carbon, pH, and SOM, according to the NMDS ordination (Fig. 3). While the total carbon and pH were positively correlated with the *Silene* communities, the SOM was located between the *Silene* communities and *Cassiope* communities. In contrast, the *Dryas* communities were negatively correlated with the total carbon and SOM.

The difference in EC between the dominant plant types and bare soil was significant from the results of Welch's ANOVA (Table 1). Despite no significances, the total carbon from the *Silene* group was likely to be high, which was similar to the NMDS result. The arrow of the SOM in the NMDS is located in the middle of the *Silene* and *Cassiope* communities. In Table 1, the *Silene* and *Cassiope* communities have the same value of total nitrogen (0.50%). Also, the SOM from the *Cassiope* community appears high. Overall, the result of the relationship between the vegetation group and soil-chemical properties from Figure 3 and Table 1 shows similar trends.

Patch area and height of the three dominant plants

Cassiope and *Dryas*, both with prostrate mat growing

Table 1 Soil-chemical properties of three dominant plant types and bare soil

Group	Bare	<i>Cassiope</i>	<i>Dryas</i>	<i>Silene</i>
Sample number	17	29	20	35
C (%)	9.1 ± 1.5	6.5 ± 0.6	5.0 ± 0.8	9.2 ± 1.4
N (%)	0.47 ± 0.6	0.50 ± 0.05	0.39 ± 0.04	0.50 ± 0.04
SOM (%)	5.3 ± 0.6	5.9 ± 0.3	4.6 ± 0.4	5.5 ± 0.3
EC ($\mu\text{S}\cdot\text{cm}^{-1}$)	105 ± 13^a	62 ± 4^b	46 ± 6^b	59 ± 5^b
pH	5.87 ± 0.19	5.57 ± 0.04	5.83 ± 0.10	5.78 ± 0.09

Values are presented as number only or mean $\pm$ standard error.

Different letters (superscript a and b) mean significant differences according to a parametric unbalanced ANOVA (Welch's ANOVA) followed by Games-Howell honest significant difference for post hoc comparisons ($p < 0.05$).

C: total carbon; EC: electrical conductivity; N: total nitrogen; SOM: soil organic matter; Bare: bare soil; *Cassiope*: *Cassiope tetragona*; *Dryas*: *Dryas octopetala*; *Silene*: *Silene acaulis*.

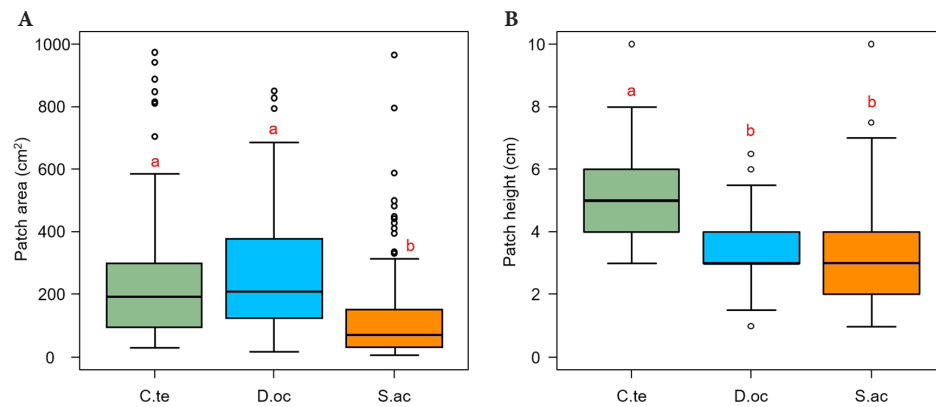


Fig. 4 Boxplots depicting the (A) patch area and (B) patch height of *Cassiope tetragona* ($n = 116$), *Dryas octopetala* ($n = 94$), and *Silene acaulis* ($n = 206$) patches. Different letters (superscript a and b) mean statistical differences ($p < 0.05$), as determined by a parametric unbalanced ANOVA using Welch's F ratio. The significance of differences ($p < 0.05$) between the means of three communities were assessed using Games–Howell honest significant difference for post hoc comparisons. The central horizontal lines within the boxes indicate the medians; the box edges indicate the quartiles; the whiskers indicate the minimum and maximum values; and the open circles indicate outliers. C.te: *Cassiope tetragona*; D.oc: *Dryas octopetala*; S.ac: *Silene acaulis*.

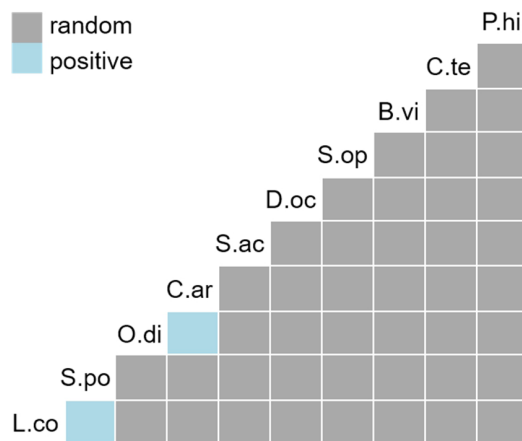


Fig. 5 Species co-occurrence matrix defined by the “cooccur” package in R software. The positive and random species associations were determined by the probabilistic co-occurrence model for 10 plants, excluding seven species with less than 1% of the importance value. Species names are positioned to indicate the columns and rows that represent their pairwise relationships with other species. P.hi: *Pedicularis hirsuta*; C.te: *Cassiope tetragona*; B.vi: *Bistorta vivipara*; S.op: *Saxifraga oppositifolia*; D.oc: *Dryas octopetala*; S.ac: *Silene acaulis*; C.ar: *Cerastium arcticum*; O.di: *Oxyria digyna*; S.po: *Salix polaris*; L.co: *Luzula confusa*.

forms, had significantly wider patch areas ($313 \pm 29 \text{ cm}^2$ and $259 \pm 23 \text{ cm}^2$, respectively) than that of *Silene* ($118 \pm 10 \text{ cm}^2$), which has a cushion and dome form (Fig. 4A). In addition, the height of *Cassiope* was higher ($5.1 \pm 0.1 \text{ cm}$) than that of *Dryas* and *Silene* ($3.4 \pm 0.1 \text{ cm}$ and $3.2 \pm 0.1 \text{ cm}$, respectively) (Fig. 4B).

Species co-occurrence pattern and richness

A total of 45 species pair combinations, with 10 species having more than a 1% importance value, were analyzed based on species presence/absence. From the co-occurrence matrix, two positive co-occurrences are represented: *Oxy-*

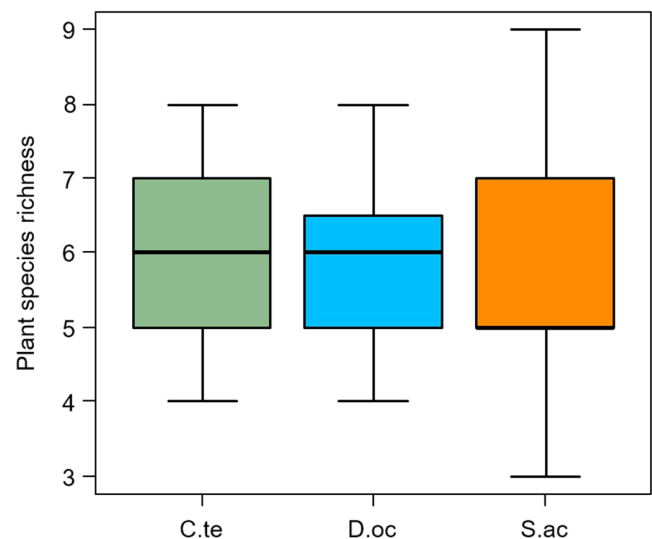


Fig. 6 Boxplots depicting plant species richness of *Cassiope tetragona* ($n = 29$), *Dryas octopetala* ($n = 20$), and *Silene acaulis* ($n = 35$) groups. Statistical analysis is carried out according to a parametric unbalanced ANOVA (Welch's ANOVA), followed by a test of Games–Howell honest significant difference for post hoc comparisons. Plant richness does not significantly differ between the dominant plant communities. The central horizontal lines within the boxes indicate the medians; the box edges indicate the quartiles; and the whiskers indicate the minimum and maximum values. C.te: *Cassiope tetragona*; D.oc: *Dryas octopetala*; S.ac: *Silene acaulis*.

ria digyna–*Cerastium arcticum* and *Luzula confusa*–*Salix polaris* (Fig. 5). Negative co-occurrences were not found and 43 random species pairs were identified at the study site. The three dominant plants did not have positive or negative co-occurrences with other plant species, distributing randomly and widely. Accordingly, the plant richness also did not significantly differ between the dominant plant communities (Fig. 6).

Discussion

I have examined plant composition structures based on the three dominant plants (*Cassiope*, *Dryas*, and *Silene*) and the soil microenvironment (daily soil-temperature range, daily soil-moisture range, and soil-chemical) in Ny-Ålesund, Svalbard. I find that the *Cassiope* and *Dryas* communities significantly reduce the daily soil-temperature fluctuation in comparison with bare soil. In particular, *Cassiope* provides the strongest buffer against the daily soil-temperature fluctuations, as compared to *Dryas* and *Silene*. In addition, the three dominant plants *Cassiope*, *Dryas*, and *Silene* are not only widely distributed at the study site, but they also have a distinctive species compositional structure.

Two Arctic-plants buffer soil-temperature fluctuations

In the particularly harsh physical environment of Ny-Ålesund, Svalbard, the two Arctic plants *Cassiope*, *Dryas* appear to offer positive effects on microhabitats, specifically regarding soil-temperature stability. My results also show that the magnitude of temperature buffering effects provided by *Cassiope* and *Dryas* differ, with more pronounced effects on stabilizing soil-temperatures associated with *Cassiope* than with *Dryas*.

Even though soil-temperatures were measured for only 1 week using two measurement devices, this research shows that *Cassiope* and *Dryas* create thermally buffered soil microhabitats. The thermal buffering in physically harsh environments is most likely due to the insulation characteristics of the thick, dense layer of live plants and dead plant litter (Badano et al. 2006), thus reducing direct heat shock and mortality of the plants living among the nurse plants (Cavieres et al. 2006). This buffering effect on soil-temperature fluctuation modifies abiotic environmental conditions towards more stable microhabitats (Cavieres et al. 2014). In Arctic ecosystems, such modifications are especially important regarding temperature because temperature is a vital factor influencing plant survival and reproduction (Badano et al. 2006). As previously mentioned, a high level of abiotic stress may strengthen the importance of plants serving as facilitators or drivers of the plant-community composition in northern latitudes (Klanderud and Totland 2004).

Previous studies have demonstrated that different kinds of Arctic plants keep soil-temperatures stable and warm. For example, Molenda et al. (2012) found that on a microclimatic scale, *S. acaulis* ameliorated stressful conditions for plants and invertebrates living inside it by buffering high temperatures and low humidity. Another nurse plant, *Azorella monantha*, maintains 5–9°C warmer microhabitats in the high-Andean ecosystem (Badano et al. 2006). Cavieres et al. (2006) have pointed out that the nurse plant

Laretia acaulis acts as a buffer against environmental temperature fluctuations in the Andes of central Chile. Also, other nurse plants in the Andes (*Azorella julianii* and *Arenaria musciformis*) appear to reduce temperature fluctuations by decreasing the daily temperature maxima (Hupp et al. 2017). In alpine environments, *Azorella aretioides*, known as a nurse plant with a cushion growth form (Cavieres et al. 2005), has buffering effects on temperature (Ecuador, 4,700 m a.s.l.), mitigating the maximum temperature during the day and increasing the minimum temperature at night (Anthelme et al. 2014).

The buffering effect of the daily soil-temperature fluctuation of *Silene*, which is known as a nurse plant, was expected to be shown in this research; however, it was not seen, which was likely due to the size of the plant. Despite the limitation of the short measurement period (7 days) and replicative numbers, this is likely to result from the patch area and height of *Silene*, which was significantly lower than that of *Cassiope* and *Dryas* (Fig. 4). According to Castro et al. (2002), the nursing effect on the lower soil-temperature and higher soil-moisture provided by plant cover (patch area) was clearly presented inside and at the edge of *Salvia lavandulifolia* as a nurse plant. In addition, the height of *Silene* in this study was rather low compared to the 2–8 cm height described by Oh and Lee (2021).

Unlike soil-temperature, there are no distinctive buffering effects of the three dominant plants on soil-moisture stabilization. This is consistent with the findings by Hupp et al. (2017), who showed that the nurse plant *Arenaria musciformis* does not have a significantly positive effect on the soil water content. On the contrary, the high-Andean cushion plant *Azorella monantha* reduces soil-moisture evaporation compared to bare soil and leads to higher water availability beneath its canopy (Badano et al. 2006). My results may be partly due to not continuously performing measurements during the field experiment because of mechanical defects and detection limits.

Soil-chemical properties related to three plant communities

Soil organic matter, total carbon, total nitrogen, and pH in soil are not associated with different dominant plant communities. Interestingly, the EC in bare soil without vegetation is significantly higher than that in the three dominant plant communities. At the study site, the presence of wild animals (e.g., Svalbard reindeer, Arctic fox) eating Arctic plants is frequent and animal feces can be found on the surface of bare soil (Hayashi et al. 2014; Son and Lee 2022). In particular, the impacts of Svalbard reindeer (*Rangifer tarandus platyrhynchus*) on vegetation resulting from trampling disturbance, grazing pressure, and the excretion of waste are detrimental for vascular plant reproduction (Cooper 2006; Hayashi et al. 2014). Svalbard reindeer and barnacle geese (*Branta leucopsis*) feed on

graminoids, forbs, prostrate plants, and bryophytes, and *Salix* is the most detected genus in their feces (Kim et al. 2022). Animal feces affect carbon and nitrogen cycles in the tundra (Hayashi et al. 2014; Olofsson et al. 2004) and can be important vectors for the transfer of environmental elements containing high organic matter and metal concentrations (Lin et al. 2009; Pacyna et al. 2019). Therefore, bare soils without vascular plants have similar or higher values of soil organic matter, total carbon, and total nitrogen compared to that of different dominant plant communities.

In this study, the live plants and dead plant litter of the three dominant plants did not improve the soil nutrients. A similar finding has been reported by Badano et al. (2006), who investigated a nurse plant, *Azorella monantha*, that was shown to have no detectable facilitative effects on soil macronutrients (i.e., nitrogen, potassium, and phosphorus). Contrarily, it has been reported elsewhere that plant species from the *Dryas* genus increase soil organic matter and the associated nitrogen in Glacier Bay, Alaska, providing more suitable microhabitats for the establishment of other plants (Chapin et al. 1994). In addition, Chen et al. (2015) found evidence that the soil beneath two nurse plants, *Potentilla articulata* and *Arenaria polytrichoides*, contains higher concentrations of nitrogen and potassium than the sites at which these nurse plants are absent. Moreover, the soil within patches with nurse plants forming compact and large cushions had much higher nutrient, organic matter, and soil water contents than that of the bare ground (Nuñez et al. 1999; Schöb et al. 2013).

Based on the NMDS result, although there were significant relationships between the three plant community structures and soil-chemical properties, the blue arrow of the soil SOM was located between the *Cassiope* and *Silene* communities. This is consistent with the result in Table 1, which shows a slightly similar SOM value in the *Cassiope* and *Silene* communities.

Regarding soil nutrients, the facilitative effects of plants are unlikely to prevail because limited nutrients are shared via competition or interference with other plants (Padilla and Pugnaire 2006). Additionally, plants compete with soil microbes for soil nitrogen in unproductive soil (Bardgett et al. 2003). In tundra, the carbon output to the soil and decomposition are too slow to detect due to poor litter quality, low temperatures, and frequent soil anoxia (De Deyn et al. 2008; Mack et al. 2004). Furthermore, patches or cushions of plants with different sizes and succession stages have different demands for soil nutrients and soil-moisture (Lu et al. 2018). These reasons contribute to explaining why the three plant communities here do not show distinctively higher soil-chemical nutrients compared to that of bare soil.

Plant-species co-occurrence pattern and richness

Three studied plants distributed widely and randomly with other plant species in Ny-Ålesund. Furthermore, species richness did not differ significantly between the three dominant plant communities. It was predicted that the *Cassiope* community, which had larger patches than those of the other two communities, may have more plant species richness because the wider the patch area, the higher the plant richness (Nuñez et al. 1999). This positive effect on species richness is largely owed to the patch-level modification of the abiotic environment by plants with cushion life-forms, which facilitates the recruitment, survival, and growth of many plant species (Cavieres et al. 2007; Gavini et al. 2020). To accurately determine the plant-plant interaction, such as facilitation or competition, a comparison experiment for plant richness between patches and cushions should have been conducted (Piper et al. 2019). Moreover, co-occurrence analysis is based on plant presence/absence patterns, meaning that only the frequency in communities is calculated without counting the individual abundance (Gu et al. 2021). Accordingly, to better understand the plant-plant interactions and co-occurrence patterns, precise experimentation, replicated studies across a wider range of species combinations, and analyses considering plant cover or abundance are necessary (Angers-Blondin et al. 2018).

Based on the NMDS (Fig. 3) and species co-occurrence matrix (Fig. 6), *Luzula confusa* (Juncaceae) and *Salix polaris* (Salicaceae) coexist at the study site. These species are distributed widely and are major components with a greater biomass (Van der Wal et al. 2000). Similar to these results, Park et al. (2018) examined the dominant plant species in Ny-Ålesund, which were classified into the following three groups, while simultaneously considering species abundance and niche overlap: Group 1 (*L. confusa* and *S. polaris*), Group 2 (*Saxifraga oppositifolia*, *B. vivipara*, and *S. acaulis*), and Group 3 (*D. octopetala* and *C. tetragona*). In addition, *O. digyna* (Polygonaceae) also occurs in diverse habitats at elevations from sea level to 4,500 m throughout the Arctic and in the mountain range (Wang et al. 2016).

Previous research about plant-plant interactions (the nurse effect, in particular) have shown that certain plants favor the establishment and survival of the associated plant species by modifying the local environment (Nuñez et al. 1999). Nurse plants can provide facilitative effects on seedling establishment and survival within or under their canopies (Cavieres et al. 2007) by creating more favorable microhabitats for other plant species than what is offered by the surrounding environment (Chen et al. 2015). *Cassiope tetragona* has also been reported to promote the growth of the alpine/sub-Arctic plant *Carex bigelowii*: when it grows near *Cassiope*, it shows increased leaf lengths and culm heights as compared with plants growing more than 20 cm

away (Carlsson and Callaghan 1991). Similarly, Klanderud and Totland (2004) found that on Svalbard, *Dryas octopetala* has a facilitative effect on the richness of Bryophytes, while it does not significantly alter the richness of vascular plants and lichen. In addition, *Dryas* heath in Norway has a dense vegetation cover (~80%) and high species diversity, thus promoting species interactions (Olsen and Klanderud 2014).

On the other hand, Boulanger-Lapointe et al. (2016) suggested that *Cassiope tetragona* may inhibit *Salix arctica* growth in Greenland, by releasing secondary metabolites. Grau et al. (2014) showed that patches of *Dryas octopetala* × *intermedia* have a distinct negative effect on small-scale plant richness. *Silene acaulis* in Ny-Ålesund showed all interactions (positive, negative, and neutral effects on species richness) according to the different aspects (Oh and Lee 2021). Therefore, to fully understand species co-occurrence, focusing on either facilitation or competition independently may be inadequate (Losapio et al. 2021). In fact, both facilitation and competition must be considered to obtain a realistic view of the interactions in Arctic plant communities in response to environmental changes (Olofsson 2004).

Kapfer and Grytnes (2017) reported that the climatic warming in the high Arctic has contributed to significant changes in the vegetation on Svalbard over the past 85 years. Dwarf shrubs, such as *Cassiope* and *Dryas*, have expanded during the last decades in the Alpine, sub-Arctic, and Arctic ecosystems (Grau et al. 2014), and the increase in shoot length growth of *Cassiope* in Svalbard may be due to Arctic climate warming (Rozema et al. 2009; Weijers et al. 2010). Higher temperatures can lead to a shift from facilitative to competitive effects in plant communities and may thus upset the current balance between these effects among Arctic plants (Callaway et al. 2002). Therefore, if temperatures in the Arctic continue to rise gradually, increasing temperatures will increase productivity and plant cover, and competition in plant communities will generally be more dominant where conditions are more physically stressful (Bhatt et al., 2010). Increasing temperatures are expected to result in drying soils in areas located close to late-melting snow patches, which will ultimately lead to a decrease in local plant diversity (Nabe-Nielsen et al. 2017). In addition to decreasing species diversity due to climate warming, shrub expansion may amplify species turnover and local extinction rates (e.g., placing Arctic forbs at risk of extinction) (Mod and Luoto 2016). Since the Arctic and alpine ecosystems are predicted to be the most sensitive to global warming (Guisan and Theurillat 2000), a shift in the patterns of species co-occurrence and interactions there should be studied.

Conclusions

Plant compositional patterns can be driven by both biotic and abiotic conditions in Arctic ecosystems. The soil-temperature under *Cassiope* and *Dryas* undergoes fewer fluctuations, which is likely to be related to wider patch areas that insulate the soil from cold air temperatures, as compared to *Silene*. In addition, the three dominant plants *Cassiope*, *Dryas*, and *Silene* are not only widely distributed at the study site, but also have a distinctive species compositional structure, although they do not differ in species richness at the study sites. To further elucidate the magnitude of the facilitative effects of the three studied Arctic plants in future research, their functional, morphological (e.g., size of the nurse plant or compactness of its canopy), and physiological traits (e.g., specific leaf area) should be considered (Anthelme et al. 2017; Schöb et al. 2013).

Supplementary Information

Supplementary information accompanies this paper at <https://doi.org/10.5141/jee.23.002>.

Table S1. Soil-temperature from 12 July 2015 to 18 July 2015. **Table S2.** Soil-moisture content from 12 July 2015 to 18 July 2015. **Table S3.** The list of surveyed plants.

Abbreviations

ANOVA:	Analysis of variance
Bare:	Bare soil
B.vi:	<i>Bistorta vivipara</i>
C:	Total carbon
C.ar:	<i>Cerastium arcticum</i> ; <i>Cassiope</i>
C.te:	<i>Cassiope tetragona</i> ; <i>Dryas</i>
D.oc:	<i>Dryas octopetala</i>
EC:	Electrical conductivity
HSD:	Honest significant difference
L.co:	<i>Luzula confuse</i>
N:	Total nitrogen
NMDS:	Non-metric multidimensional scaling
O.di:	<i>Oxyria digyna</i>
P.hi:	<i>Pedicularis hirsuta</i> ; <i>Silene</i>
S.ac:	<i>Silene acaulis</i>
SOM:	Soil organic matter
S.op:	<i>Saxifraga oppositifolia</i>
S.po:	<i>Salix polaris</i>

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Availability of data and materials

The datasets are available from the corresponding author on reasonable request.

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Not applicable.

Consent for publication

Not applicable.

Competing interests

The author declares that they have no competing interests.

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