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Impact of erect shrubs on the cover and fruit productivity of berry species in subarctic Canada

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Abstract

Berry species are an important source of food in late summer for resident and migrant animals, and an integral part of the diet and culture of Indigenous Peoples. This study investigated how the presence of erect shrub patches (cover > 25%) affected the occurrence, cover, and fruit productivity of *Vaccinium uliginosum* L., *Vaccinium vitis-idaea* L., and *Empetrum nigrum* L. in the vicinity of Umiujaq, a subarctic community that has experienced a rapid increase in erect shrub cover since the 1990s. Our results indicated that berry species are ubiquitous in the area although the likelihood of occurrence is nearly three times lower under shrub patches. The cover and fruit productivity of *V. uliginosum* and *E. nigrum* diminished under erect shrub patches and this effect was more pronounced at the center of patches. In contrast, the cover and fruit productivity of *V. vitis-idaea* was not influenced by the presence of erect shrub patches. Finally, erect shrub patches delayed fruit ripening for *V. uliginosum* and *V. vitis-idaea* but differences could not be measured for *E. nigrum*. This study suggests that observed and forecasted increases in erect shrub cover in the Arctic may have widespread negative impacts on berry species.

Key words: berry, climate change, shrubification, subarctic, *Vaccinium*, Umiujaq

Introduction

In low Arctic ecosystems, the biomass of erect shrubs is increasing under warming temperatures (Elmendorf et al. 2012; Myers-Smith et al. 2015). This trend, also referred to as "shrubification" or vegetation greening (Myers-Smith et al. 2020), is associated with new recruitment (Davis et al. 2021), increases in annual growth (Forbes et al. 2010), and foliage production (Bonta et al. 2023). It has been linked to vegetation indices or spectral greening as detected by remote sensing studies (Berner et al. 2020). While heterogeneity in response is widespread (Myers-Smith et al. 2020), the change in plant community composition and canopy cover is having consequences on local ecosystems with notable impacts on snow cover (Liston et al. 2002; Pomeroy et al. 2006), soil temperatures (Walker et al. 2003; May et al. 2022), nutrient cycling (Cornelissen et al. 2007; Buckeridge et al. 2010), and carbon balance (Mekonnen et al. 2021; Schuur et al. 2022).

At the plant community-level, the increase in erect shrub cover has a range of effects including positive and negative interactions with neighboring plants (Bråthen and Lortie 2016). The larger deciduous leaves and enhanced canopy height directly compete with prostrate plants for light (Chapin et al. 1995). The newly established vertical structure also modifies air circulation, buffering temperatures and increasing seed and particle trapping (Bråthen and Lortie 2016). In summer,

erect shrub patches form a protective barrier against wind abrasion and in winter they shelter low-lying plants under a thicker cover of snow allowing plants to establish beyond their climate optimum (Sturm et al. 2005). The expansion of erect shrub cover has been associated with a widespread decrease in cryptogam species and lichens and an increase in forbs, while the response of other plant functional groups is more variable (Pajunen et al. 2012; Crofts et al. 2018; Chagnon and Boudreau 2019).

Prostrate berry species are common in the low Arctic and within the forest-tundra ecotone where they are an important source of food for humans and animals. Berry picking is a traditional activity of nutritional and cultural significance for Indigenous Peoples around the circumpolar Arctic (Boulanger-Lapointe et al. 2019; Markkula et al. 2019; Hill et al. 2023). The abundance of fruits during a short period also benefits a wide range of animals including voles (Krebs et al. 2010), passerines (Norment and Fuller 1997), ptarmigans (Weeden 1969), and bears (Hébert et al. 2008; Edwards et al. 2011). Berries constitute a large proportion of the Canada and cackling geese diet during late summer providing crucial pre-migratory nutrition (Cadieux et al. 2005; Hupp et al. 2013).

Although berry species are an important component of Arctic socio-ecological systems, the impact of recent environmental changes on their growth and reproduction is poorly

Fig. 1. Study region (inset) and location of the study sites in the vicinity of Umiujaq, Nunavik (Quebec, Canada). Maps were created in QGIS (version 3.28); inset uses the *Administrative Boundaries in Canada* vector file (Government of Canada 2021; NAD83), and the main map is a Sentinelle 2 raster image (taken on 23 July 2021; NAD83) with field study sites location (red points).
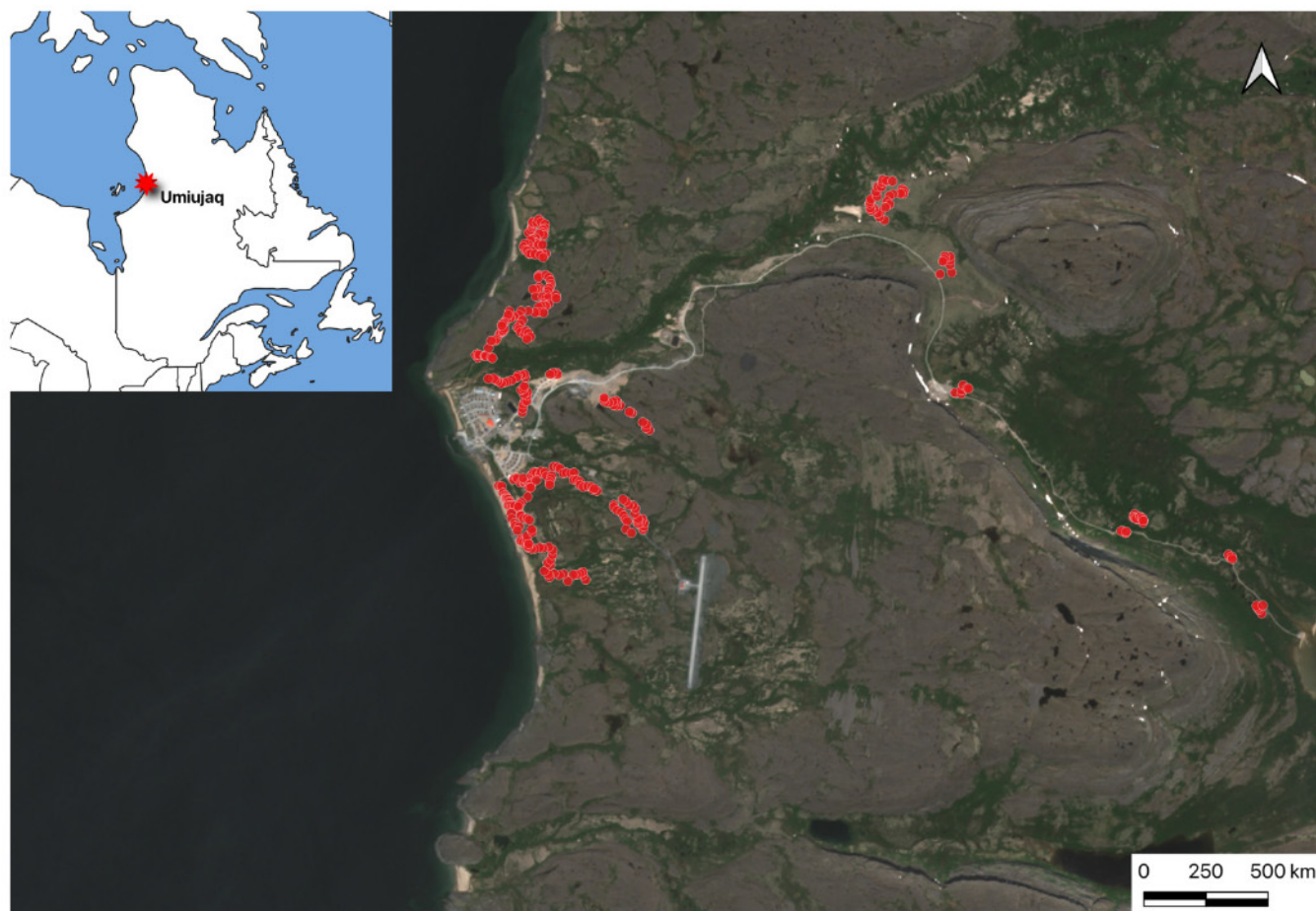
documented in the Canadian Arctic. Local and Indigenous observations suggest that erect shrubs are competitively excluding berry species with some traditional harvesting sites overgrown with erect shrubs (Cuerrier et al. 2015; Gérin-Lajoie et al. 2016). These observations are congruent with studies near the treeline in Scandinavia showing that berry species produce more flowers when located in open relative to forested habitats due to higher radiation and decreasing apical dominance (Tolvanen 1995; Elisabetta et al. 2013). Shading experiments found similar responses with delayed phenology and a decline in the abundance of flowers with increasing shade for *V. vitis-idaea* and *Arctous alpina* (L.) Nied (May et al. 2022). Whether flowers produce viable fruits will depend on pollination success. Fruit set (i.e., the ratio of berries to flower) increases with pollinator activity, which is shaped by local environmental conditions (Parkinson and Mulder 2020). When comparing adjacent forested and open habitats, studies found both positive (Boulanger-Lapointe et al. 2017) and negative (Siegwart Collier 2020) impacts of tree cover on fruit set in berry species. Meanwhile, the influence of shrub canopy cover on pollinator activity in tundra environments is largely unknown (McDermott et al. 2021). The decline in flower production with increasing erect shrub cover is thus the main documented mechanism by which these shrubs may limit the production of berries.

In this study, we asked a simple question for the species of interest: is the presence of erect shrub patches (cover > 25%) limiting the performance (occurrence, cover, fruit productivity, and ripening) of *Empetrum nigrum* L. (crowberry), *Vaccinium uliginosum* L. (blueberry), and *Vaccinium vitis-idaea* L. (cranberry) in tundra ecosystem? We hypothesized that no matter the underlying environmental conditions, the presence of erect shrub patches will always reduce the overall performance of prostrate berry species in otherwise favourable habitats. Therefore, we predicted that the occurrence, the cover, and the fruit productivity of berry species will decrease along a transect extending from the open tundra to a close erect shrub canopy.

Materials and methods

Study area

The study was conducted near the Inuit community of Umiujaq, Nunavik (56°33′07″N, 76°33′57″W, Fig. 1). Mean annual temperature in Umiujaq was −3.0 °C for the period 1998–2022 (CEN 2024). Snow cover during winter has an average

Fig. 2. Site location methodology, using displacement of a random distance (ranging from 20 to 40 m) along a random bearing (0°–180°), and sampling design along a transect extending from the open tundra (Q1) to the center of the shrub patches (Q4). A total of 352 sites (1402 quadrats) were sampled near the Inuit community of Umiujaq (56°33′07″N, 76°33′57″W).
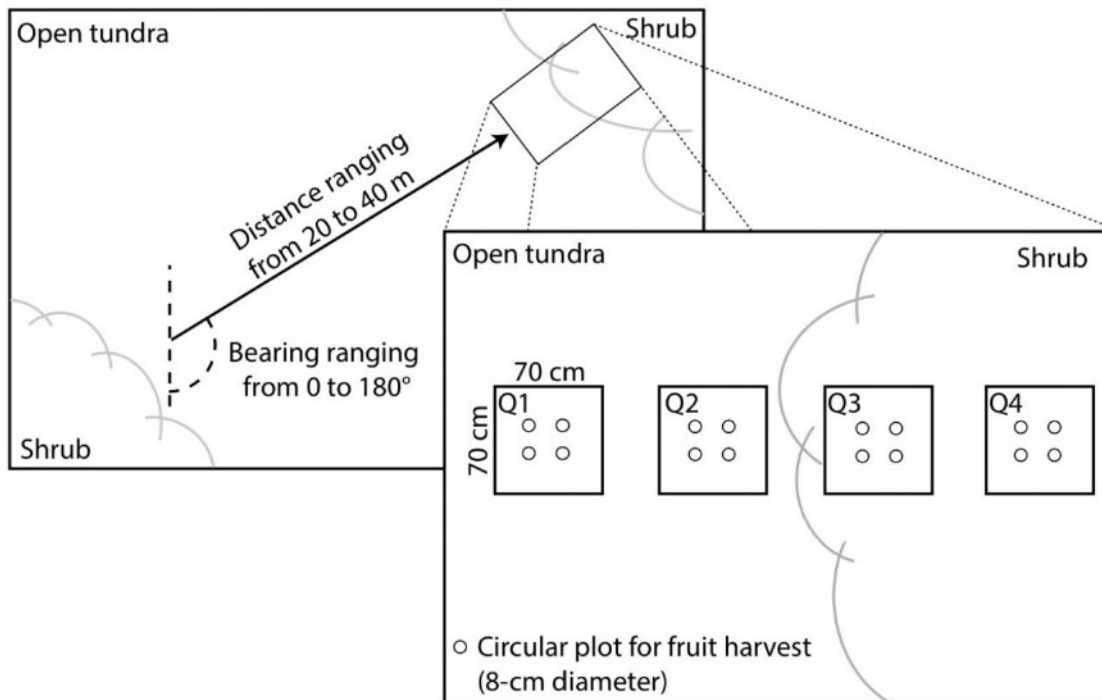
thickness of ca. 50 cm, although it is greater under and near erect shrubs (Domine et al. 2015; Paradis et al. 2016). Strong winds, from the Hudson Bay (west and northwest), during winter can reach >100 km h^{-1} (Fortier et al. 1994). Over the last few decades, warmer air temperatures have triggered rapid permafrost degradation (Payette et al. 2004; Pelletier et al. 2019).

The study area is located at the forest-tundra ecotone (Payette 1983), within the discontinuous permafrost zone (Allard and Seguin 1987). It is characterized by shrub tundra dominated by *Betula glandulosa* Michx. In sheltered areas, black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb) can form dense clumps of trees and krummholz. Dense patches of *Alnus viridis* ssp. *crispa* (Aiton) Turill occur in moist to wet areas at the margin of running water. The proportion of land covered by erect shrubs increased by 12% between 1994 and 2010 (i.e., from 24% to 31%; Provencher-Nolet 2014) and conservative models indicate that this cover may double over the next 50 years (Lemay et al. 2018). Umiujaq is known as a prime location for berry picking and people travel to the community at the end of the summer to participate in the annual Blueberry Festival (Boulanger-Lapointe et al. 2019).

Study species

The berry species studied are all woody prostrate shrubs in the Ericaceae family. They have a circumpolar distribution and range from the forest-tundra ecotone to sheltered areas in the high Arctic (Aiken et al. 2007). *Empetrum nigrum* is a low (5–30 cm: Aiken et al. 2007) creeping species with horizontal stems that form dense mats. Leaves are evergreen and needle-shaped; fruits are dark purple to black. In the Arctic, *E. nigrum* is often reported on rocky or gravelly slopes (Aiken et al. 2007). In the boreal forest, it can dominate the understory (Nilsson and Wardle 2005). *Vaccinium vitis-idaea* is an evergreen species that produces white to pink flowers and spherical bright red fruits. It is often observed growing in well-drained to dry habitats. There are large interannual variations in the timing of flowering, berry production, and abundance for this species (Langvall and Löfvenius 2021). *Vaccinium uliginosum* is a deciduous species with small oval and glabrous (i.e., smooth) leaves that grows on moderately to well-drained flat terrain and shallow slopes (Aiken et al. 2007). Flowers are pink and bell-shaped; fruits are dark blue. *Vaccinium uliginosum* tends to flower earlier than *V. vitis-idaea* (Khorsand et al. 2024).

Field measurements

Sampling locations ($n = 352$, Fig. 1) were selected near the community on the coast and in the Tasiapik Valley to the east. An initial random location was chosen within a range of well-drained and mesic sites where berry species are usually most abundant (Fig. 2). At this location, a vector with a direction (0°–180°) and length (20–40 m) determined using a random table was walked. Upon reaching the end of the vector, the nearest erect shrub patch was selected to establish the monitoring transect. A transect was only established if the following criteria were met: (1) there was an erect shrub patch no farther than 10 m away from the end of the vector, (2) there was an erect shrub patch with >25% cover and a diameter > 2 m, and (3) the area was suitable for at least one of the berry

species (i.e., did not present a dense herbaceous vegetation or only a continuous stand of erect shrubs and/or trees).

In July 2015, the cover of berry species (i.e., *E. nigrum*, *V. uliginosum*, and *V. vitis-idaea*) and erect shrubs (e.g., *Alnus viridis*, *B. glandulosa*, and *Salix calcicola* Fernald & Wiegand) was assessed at each transect (*n* transect = 352) within four 70 cm × 70 cm quadrats (*n* quadrat = 1408, Fig. 1). Quadrats were placed as follows: (Q1) in the open tundra at a distance of ≥70 cm from any erect shrub patch (>25% cover), (Q2) in the open tundra, adjacent to the margin of the erect shrub patch, (Q3) at the margin of the erect shrub patch, and (Q4) inside the erect shrub patch, at ≥70 cm from the margin, referred to afterwards as the center of the patch. The cover of berry and erect shrub species was assigned a 5% cover class (0%–5%, 5%–10%, etc.) at all sampling sites. The cover of all erect shrub species was pooled and used to define patches, i.e., continuous areas with erect shrub cover > 25%.

At the end of August, 299 (*n* quadrat = 1196) of the 352 transects were randomly selected for fruit collection. This generally corresponds to the time when fruits start ripening before the local berry picking festival. It was not possible to assess the importance of animal consumption on our plots. Fruits were harvested inside four circular plots of 50 cm² (8 cm diameter) placed at equidistance inside the quadrats previously used to evaluate species cover (Fig. 1). Fruits from each circular plot were pooled by quadrat, they were counted, sorted by ripening stage (1: green; 2: partially ripe, i.e., hard fruit partially green; 3: ripe, i.e., soft fruit and dark color; 4: withered), and weighed fresh and dry (after 48 h at 60 °C). Fruit productivity was expressed as dry fruit biomass per area (g/m²). We created an index to assess the difference in ripening between plots using the following formula:

$$(1) \quad \text{Ripening index} = \frac{(n \text{ stage } 2 * 0.5) + (n \text{ stage } 3 * 1)}{n \text{ total fruit}}$$

where "*n* stage 2" is the number of berries in ripening stage 2, "*n* stage 3" is the number of berries in ripening stage 3, and "*n* total fruit" is the total number of fruits in stages 1–4.

Statistical analyses

The occurrence of berry species was calculated as the percentage of quadrats (1) where species were present and (2) where species were present and produced berries. A chi-square independence test (balanced, *n* = 352) was used to determine whether differences along the transect were significant. To determine differences among pairs of quadrats, we performed a posteriori paired comparisons (chi-square) test corrected for multiple comparisons to account for the structure of the experimental design (MacDonald and Gardner 2000).

Since the normality assumption was not met for the species cover and fruit productivity, a two-factor Friedman test was used to assess differences among quadrats for those variables (Friedman 1937; Hollander and Wolfe 1999). We then used a post hoc test of Wilcoxon, Nemenyi, and McDonald–Thompson with 2500 Monte Carlo iterations to assess which pairs of quadrats were significantly different (package *NSM3*; Hollander and Wolfe 1999). The statistics use average ranks

to avoid issues with ties among observations (Hollander and Wolfe 1999).

Due to the low number of sites with fruits of the same species along the transect (*n* < 10), we pooled the fruits harvested in the open tundra (Q1–Q2) and under erect shrubs (Q3–Q4) to calculate the ripening index for each species (*E. nigrum*, *n* = 40; *V. uliginosum*, *n* = 71; *V. vitis-idaea*, *n* = 47). We then used a Wilcoxon test for paired data to compare fruit ripening between the open tundra and under erect shrub cover. Statistical analyses were computed using the R statistical environment, version 2.0.0 (R Core Team 2020).

Results

The study species (*E. nigrum*, *V. uliginosum*, and *V. vitis-idaea*) were common throughout the study area and completely absent in only 9% of the quadrats. These quadrats without berry species were nearly three times more common at the center of erect shrub patches than at the other three positions along the transect. The most ubiquitous species was *V. vitis-idaea*, found in 72% of the quadrats, followed by *V. uliginosum* (46%) and *E. nigrum* (34%). The three species co-occurred in 16% of the quadrats. *Vaccinium vitis-idaea* was the sole berry species found in 35% of the quadrats, far ahead of *V. uliginosum* (9%) and *E. nigrum* (3%). Erect shrub cover was on average 74% (SD = 14) at the margin of patches (Q3) and 76% (SD = 14) at the center of patches (Q4).

The occurrence of *E. nigrum* ($\chi 2 = 12.62$, $p = 0.006$) and *V. uliginosum* ($\chi 2 = 23.17$, $p < 0.001$) varied along the transect. These two species were found less frequently at the center of the erect shrub patch (Q4) than at the other three positions along the transect (Q1–Q3). The occurrence of *V. vitis-idaea* did not vary along the transect ($\chi 2 = 3.42$, $p = 0.331$). The occurrence of fruit-bearing individuals of the three species varied significantly along the transect (*E. nigrum*: $\chi 2 = 49.32$, $p < 0.001$; *V. uliginosum*: $\chi 2 = 66.62$, $p < 0.001$; *V. vitis-idaea*: $\chi 2 = 20.63$, $p < 0.001$). For *E. nigrum*, fruit-bearing individuals were less frequently observed in erect shrub patches (Q3–Q4: 12%–23%) than in the open environment (Q1–Q2: 31%–32%). For *V. uliginosum*, individuals bearing fruits were less frequent at the center of the erect shrub patch (Q4: 20%) than at the other positions (Q1–Q3: 40%–46%). Finally, for *V. vitis-idaea*, there were significantly more fruit-bearing individuals at the margin of the erect shrub patch (Q3: 46%) than at the center (Q4: 30%).

Cover, fruit productivity, and ripening

Mean cover of berry species ranged from 5% to 20% (Fig. 3b), while fruit productivity rarely exceeded 5 g/m² (Fig. 3). The cover of *E. nigrum* was lower at the center of the erect shrub patch (Q4) than at any other position along the transect (*p* < 0.001). However, fruit productivity was clearly lower both inside the erect shrub margin (Q3) and at the center of the patch (Q4) (*p* < 0.001). For *V. uliginosum*, both cover (*p* < 0.001) and productivity (*p* < 0.001) were lower inside the erect shrub margin (Q3) and at the center of patches (Q4) than in the open environments (Q1–Q2). The cover of *V. vitis-idaea* (*p* < 0.001) was higher under the erect shrub margin (Q3) than at the three other positions (Q1–Q2, Q4). However, there was a

Fig. 3. Effect of the treatment on the (*a*) cover (mean ± SE) (%, $n = 352$) and (*b*) fruit productivity (mean ± SE) (g/m², $n = 299$) for *Empetrum nigrum*, *Vaccinium uliginosum*, and *Vaccinium vitis-idaea* along a transect extending from the open tundra (Q1) to the center of the shrub patches (Q4). Different letters show significant differences between positions for each species based on a post hoc test of Wilcoxon, Nemenyi, and McDonald–Thompson; $\alpha = 0.05$).
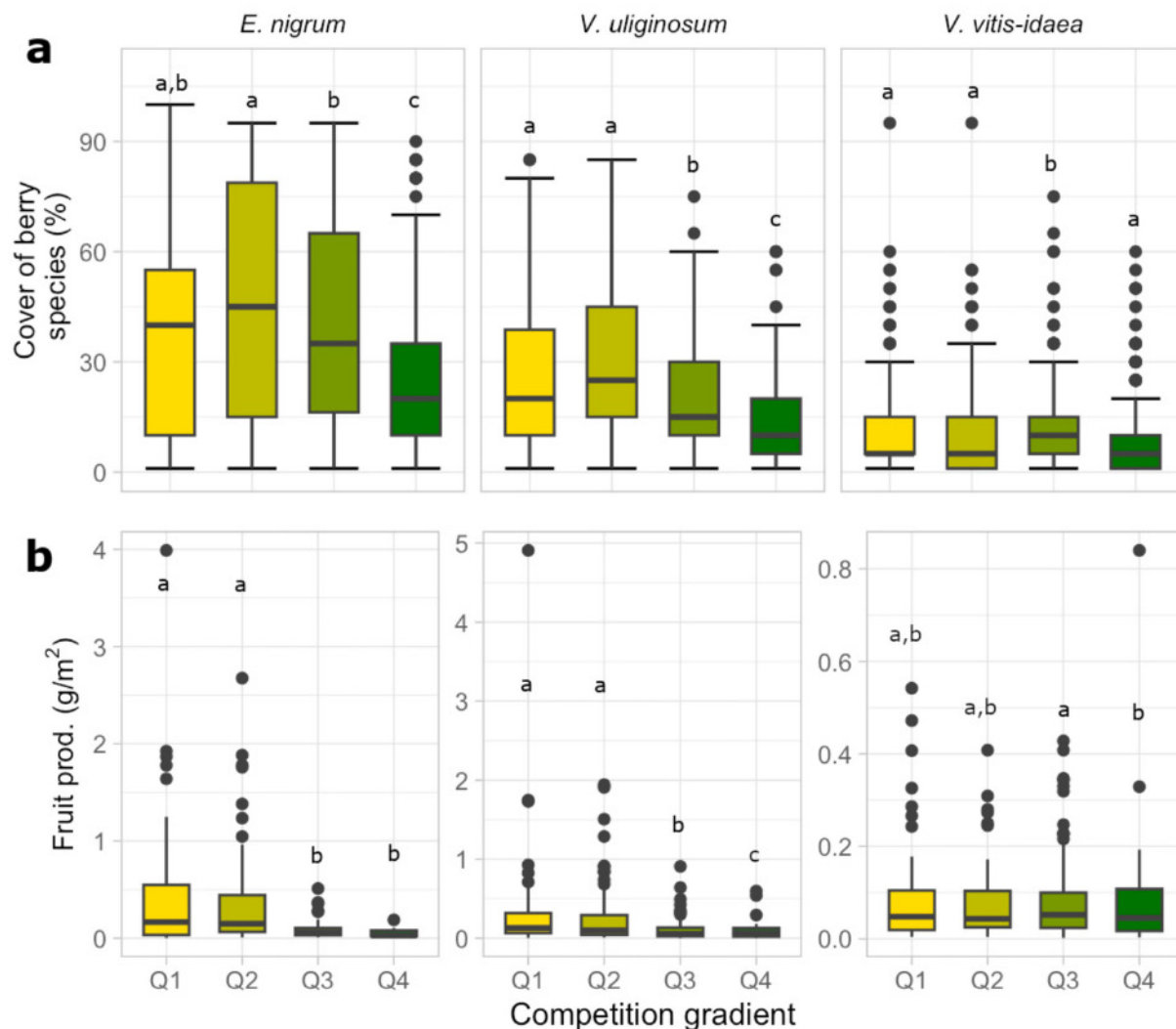
significant difference in fruit productivity only between the inside margin and the center of the patch ($p < 0.001$). At the time of measurement, most *E. nigrum* berries were ripe and no difference in fruit ripening ($p = 0.346$; Fig. 4) was measured along the transect. However, fruit ripening of both *V. uliginosum* ($p = 0.002$) and *V. vitis-idaea* ($p < 0.001$) was delayed in the erect shrub patch.

Discussion

Our results suggest that the observed and predicted increase in erect shrub cover in the Arctic may have a widespread negative impact on the availability of berries. In this study, we measured significantly lower cover and fruit productivity of *E. nigrum* and *V. uliginosum*, but not *V. vitis-idaea*, at the center of erect shrub patches in areas that are otherwise good berry patches. This trend was consistent across hundreds of sampling locations in a region recognized

both for its good berry picking and rapid increase in erect shrub cover. Our results are consistent with local observations of the impact of erect shrub cover on berry species (Cuerrier et al. 2015; Gérin-Lajoie et al. 2016) and shifts in plant functional groups, from prostrate to erect species, observed in other studies on understorey plant composition in the Arctic (Pajunen et al. 2012; Crofts et al. 2018; Chagnon and Boudreau 2019). They give some insights into the impact of biotic interactions under a warming climate.

In this study, the clearest negative impact of erect shrub cover was observed at the center of patches, and this may be due to two concurring factors. First, plant habit characterized by the presence of horizontal stems branching extensively means that measures taken at the inside margin of the patch may reflect conditions for an "individual" subsidized by ramets located outside the patch. Secondly, since erect shrub cover is rapidly increasing in the region (Provencher-Nolet 2014; Beck et al. 2015), plots at the inside margin of

Fig. 4. Ripening index (mean ± SE) of *Empetrum nigrum* ($n = 40$), *Vaccinium uliginosum* ($n = 71$), and *Vaccinium vitis-idaea* ($n = 47$) in the open tundra (OT), corresponding to Q1–Q2, and under erect shrub cover (SC), Q3–Q4. Different letters show significant differences between the two environments for each species (Wilcoxon test for paired data; $\alpha = 0.05$).
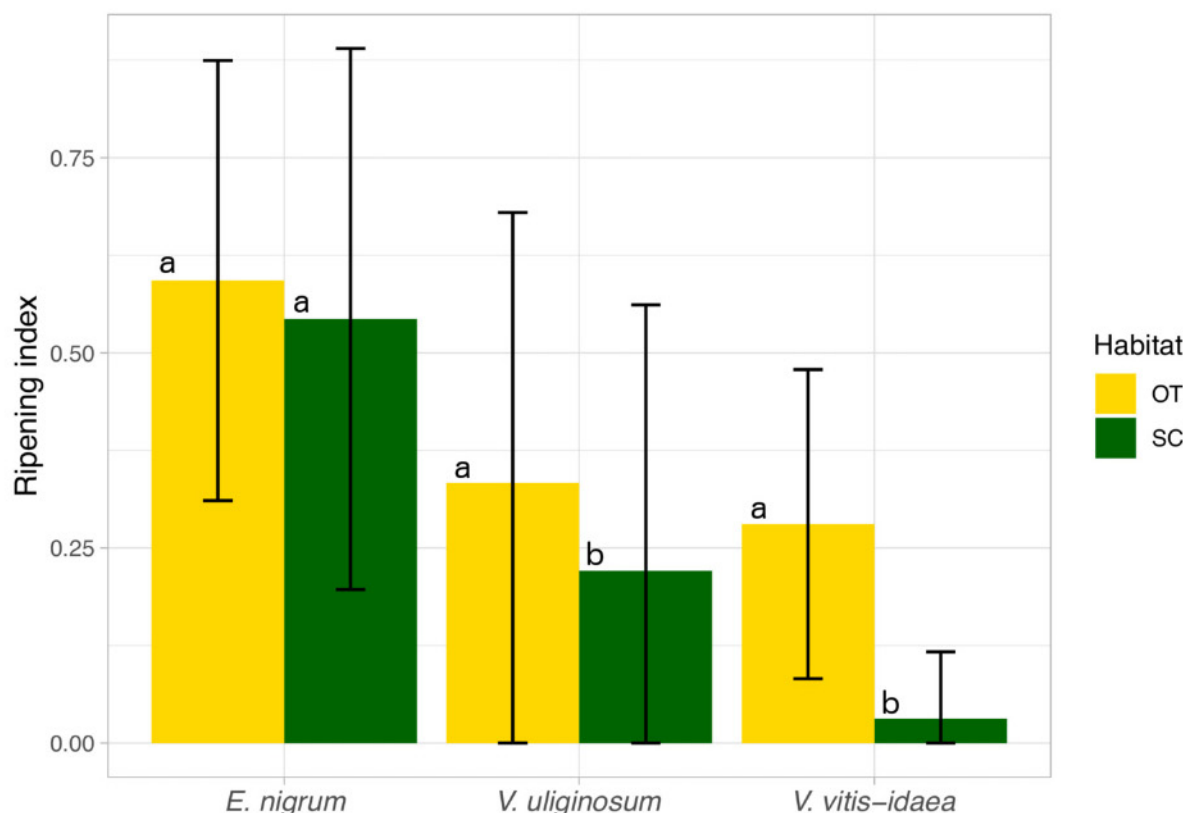
erect shrub patches may not have been experiencing interspecific competition for a long time and thus cover may still be reflecting recent more open conditions. While the transition from prostrate to erect shrubs is unlikely to lead to the exclusion of berry species at the regional level (Kitagawa et al. 2020), results from this study indicate that *E. nigrum* and *V. uliginosum* will experience a continued reduction in cover and reproductive success as the cover of erect shrubs continues to increase in the region (Lemay et al. 2018).

In terms of the impact of erect shrubs on phenology, the difference in the ripening indices for *V. uliginosum* and *V. vitis-idaea* indicated that conditions under the canopy delay fruit maturity, potentially reducing seed viability in the event of an early frost. Delayed fruit ripening is consistent with delayed peak flowering of *V. vitis-idaea* measured under experimental shading conditions (May et al. 2022). For *E. nigrum,* it is not possible to know whether the lack of difference in ripening indices indicates shade tolerance or whether differences were simply no longer visible at the time of harvest because of the species' earlier fruit ripening.

Ericaceous species, such as *E. nigrum* and *V. uliginosum*, are well known to rely heavily on clonal growth for population maintenance (Eriksson 1989; Szmidt et al. 2002). However, some studies reported frequent *E. nigrum* seedling establishment and the importance of sexual reproduction in newly formed (Boudreau et al. 2010) or eroding (Hill et al. 2012) coastal systems suggesting that a diminution in seed availability could affect population establishment and expansion.

Moreover, delayed fruit maturity may cause temporal mismatch for herbivore species relying on berries in late summer such as migratory geese (Hupp et al. 2013) and bears (Hébert et al. 2008).

While canopy cover delayed the fruit ripening of *V. vitis-idaea*, it otherwise had little impact on cover and fruit abundance suggesting a higher tolerance of this species to shading. Similarly, May et al. (2022) found that only the highest level of shading (i.e., 80%) affected flowers in *V. vitis-idaea*. They did not measure a decline under intermediary shading conditions (i.e., 40%), mirroring measurements at the margin of erect shrub patches in this study. Siegwart Collier (2020), in their study of the impact of experimental warming on *V. vitis-idaea*, *V. uliginosum*, and *E. nigrum* in Nain and Torr Bay (Nunatsiavut), found on the contrary that *V. vitis-idaea* was the only species to demonstrate a negative response in fruit production with increasing cover of *B. glandulosa*, even if the total cover of erect deciduous shrubs in their plots was less than 40%. Interestingly, Nunatsiavut receives a very large amount of precipitation during the summer compared to other Arctic locations (Rapaić et al. 2015), which may make it a unique case where increasing temperatures are not necessarily associated with drier soils (Siegwart Collier 2020). The response of *V. vitis-idaea* is particularly interesting considering recent results documenting a decline in berry species cover over the last 18–26 years in the northern boreal forest, except for *V. vitis-idaea* (Krebs et al. 2024). In this later study, climate variables were not significantly correlated to changes in cover.

The authors hypothesized that light availability may be responsible for the observed pattern, although this variable was not explicitly measured in the study. While studies using different methodologies over different timescales should be interpreted with caution, Krebs et al. (2024), Siegwart-Collier (2020), and this study all linked berry species cover to fruit productivity, but showed contrasting impact of shading on productivity, highlighting the strong control exerted by site-specific conditions. These results underline the need to investigate the impact of response time, local and regional environment changes, and their interactions to understand the mechanisms of change in berry production.

Studies across the Arctic have shown differential impacts of warming temperatures on berry species performance (Bråthen et al. 2007; Wilson and Nilsson 2009; Vowles et al. 2017; Weijers et al. 2018) and distribution (Hirabayashi et al. 2022; Hamilton et al. 2024). Hence, warming temperatures may not directly disadvantage these species, but our results indicate the potential for erect shrub patches to reduce the performance of *V. uliginosum* and *E. nigrum*. Wherever erect shrub cover is increasing, a progressive decline in the abundance of berry species may be expected north of the tree line.

Conclusion

Our results demonstrate that shifts in erect shrub abundance will have negative impacts on *V. uliginosum* and *E. nigrum* cover and fruit productivity, delay phenology of *V. uliginosum* and *V. vitis-idaea*, and potentially impact local cultural practices and resource availability for animals. The influence of erect shrubs on *V. vitis-idaea* would need to be further investigated but this study and others (May et al. 2022; Krebs et al. 2024) suggest that it may, at least in the short term, not be strongly influenced by canopy closure. Considering current predictions of an increase in erect shrub cover in the region, we can expect a further diminution in the availability of *V. uliginosum* and *E. nigrum* in the coming years. The impact on animal populations has yet to be quantified, but these changes may affect species distribution and feeding behaviour. Local harvesters will similarly have to modify berry picking routes and may not be able to return to traditional harvesting sites.

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon request.

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Supervision: SB, EL
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Competing interests

The authors declare there are no competing interests.

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