



# Climate and environmental drivers of berry productivity from the forest–tundra ecotone to the high Arctic in Canada

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**Abstract:** Berry shrubs are found across the circumpolar North where they are an important source of food for people and animals. However, the environmental controls on berry productivity in these regions is poorly understood. This study presents the results of an ongoing berry productivity monitoring program for *Empetrum nigrum* L., *Vaccinium uliginosum* L., and *Vaccinium vitis-idaea* L. from the forest–tundra ecotone to the high Arctic in Canada. Berry productivity was the highest recorded for these species with up to 119 berries/m<sup>2</sup> (*E. nigrum*) and 661 berries/m<sup>2</sup> (*V. uliginosum*) measured at one plot in Pangnirtung. On average, berry productivity for *E. nigrum* and *V. uliginosum* was higher toward the northern edge of the species distribution range. The climate variables important for the productivity of *V. uliginosum* in high Arctic sites were closely associated with the onset of the growing season and water availability during the growing season, whereas those important in the low Arctic sites reflected conditions during the growing season. None of the climate variables used were associated with the productivity of *E. nigrum* and *V. vitis-idaea*, likely due to complex responses and length of the time-series, thus highlighting the importance of continued monitoring in partnership with northern people and institutions.

**Key words:** Arctic tundra, berry, *Empetrum nigrum*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea*.

**Résumé :** Les arbustes producteurs de baies sont répandus au Nord du cercle polaire où ils constituent une source importante de nourriture pour les humains et les animaux. Malgré leur importance écologique, on connaît peu de choses quant à l'influence des facteurs environnementaux sur la productivité en fruits de ces espèces. Cette étude présente les résultats d'un programme de suivi à long terme d'*Empetrum nigrum* L., *Vaccinium uliginosum* L., et *Vaccinium vitis-idaea* L. depuis l'écotone forêt-toundra jusque dans le haut Arctique au Canada. La plus haute productivité en fruits connue pour ces espèces a été mesurée à Pangnirtung avec des valeurs pouvant atteindre jusqu'à 119 fruits/m<sup>2</sup> (*E. nigrum*) et 661 fruits/m<sup>2</sup> (*V. uliginosum*). En moyenne, la productivité en fruits d'*E. nigrum* et *V. uliginosum* était plus élevée vers la limite Nord de leur aire de répartition. Les variables

Received 22 August 2019. Accepted 27 February 2020.

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\*Greg H.R. Henry currently serves as co-Editor-in-Chief, peer review and editorial decisions regarding this manuscript were handled by Steven Siciliano and Lisa Loseto.

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climatiques importantes pour la productivité de *V. uliginosum* dans les sites du haut Arctique étaient étroitement associées au début de la saison de croissance et à la disponibilité en eau pendant la saison de croissance, tandis que les variables importantes dans les sites du bas Arctique reflétaient généralement les conditions durant la saison de croissance. Aucune des variables climatiques utilisées dans les modèles n'était corrélée à la productivité de *E. nigrum* et *V. vitis-idaea*, probablement en raison de la complexité des réponses et de la longueur des séries chronologiques, ce qui souligne l'importance d'un suivi continu en partenariat avec les communautés et les institutions du Nord. [Traduit par la Rédaction]

Mots-clés : Tundra arctique, baie, *Empetrum nigrum*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea*.

## Introduction

Berry shrubs are common across the circumpolar Arctic, providing local communities and animal species with a significant source of nutrients and vitamins (Fediuk et al. 2002; Cadieux et al. 2005; Krebs et al. 2010). In the Arctic of Canada and Alaska, berry picking is integral to the well-being and sharing practices of Indigenous communities (Simard-Gagnon 2013; Boulanger-Lapointe et al. 2019). Local knowledge holders have expressed growing concerns about the reliability of berry harvest due to declining abundance and increasing annual variability (Cuerrier et al. 2015; Hupp et al. 2015). Overall, berry shrubs produce an abundance of fruits each year, but the climatic and other environmental factors influencing their productivity are poorly understood, limiting our ability to inform decisions on land use, conservation strategies, and traditional activities in the Arctic, especially under a rapidly changing climate.

Different metrics of plant productivity are expected to reflect the influence of climate on different parts of the plant life cycle. As such, berry abundance is closely linked to reproductive effort (i.e., number of flowers produced) and pollination success, which should reflect winter and spring conditions, as well as conditions during the previous summer. The interaction of winter temperature, total precipitation, and snow cover may influence incidence of frost injuries and desiccation (Tahkokorpi et al. 2007; Taulavuori et al. 2013). Indigenous people in Alaska indicated the importance of adequate snow cover as crucial to good berry harvests, with warmer and drier winters resulting in fewer and less tasty berries (Flint et al. 2011). Spring temperature and precipitation as well as cloud cover and wind influence flower bloom and pollinator activity (Jacquemart 1997; Wipf et al. 2009; Ferland 2014; Robinson and Henry 2018). Summer conditions (warmth and water availability) strongly influence the number of pollinated flowers producing viable fruits and the size of those fruits (Kellogg et al. 2010; Selås et al. 2015). Temperature and precipitation in the previous year and two years prior influence nutrient storage and the formation of flower primordia (Selås 2000; Krebs et al. 2009).

Berry shrubs are ubiquitous in the tundra and their leaves, buds, and fruits represent a significant source of food throughout the year for Arctic animals such as rodents (Andersson and Jonasson 1986; Krebs et al. 2010; Selås et al. 2013), birds (e.g., passerines: Norment and Fuller 1997), shorebirds (McCaffery 1998), ptarmigan (Weeden 1969), and the red fox (*Vulpes vulpes*: Ehrlich et al. 2015). Ripened berries are particularly important as a main source of food in late summer for Canada geese (*Branta canadensis*: Sedinger and Raveling 1984; Cadieux et al. 2005) and grizzly bears (*Ursus arctos*: Ripple et al. 2014). Long-term monitoring studies in Fennoscandia showed that vole abundance, moth outbreaks, and climate were all important to understand the productivity of *Vaccinium myrtillus* L. (Boulanger-Lapointe et al. 2017).

An increase in erect shrub cover has been documented in many Arctic, subarctic, and alpine regions, and is expected to be one of the major effects of climate change on Arctic

terrestrial ecosystems (e.g., Sturm et al. 2001; Tremblay et al. 2012). Shrubs are growing more rapidly, existing shrub patches are infilling, and the shrub line is moving up in elevation in alpine areas and to higher latitudes in Arctic systems (Myers-Smith et al. 2011). However, erect shrubs increase shading for prostrate berry plants reducing growth and productivity (Lavallée 2013; Lussier 2016). Nevertheless, the growth of *Empetrum nigrum* L. (Buizer et al. 2012) and *Vaccinium vitis-idaea* L. (Shevtsova et al. 1997) increased in response to warming temperatures and selective herbivory may favor less palatable evergreen species in certain areas (Vowles et al. 2017).

In the context of rapid cultural, environmental and land use changes in the Arctic, an extensive research effort and community-based monitoring program was initiated in 2008 under the Canadian International Polar Year program, and continued under ArcticNet (a Network of Centres of Excellence program of Canada), to better understand the ecology and Inuit *Qaujimaqatuqangit* (i.e., the extensive knowledge and experience passed from generation to generation among Inuit: Karetak et al. 2017) of berries (Henry et al. 2012). In this study, we present the first synthesis of this ongoing research effort that brought together local knowledge holders, teachers, students, and scientists to better understand spatial and long-term trends in berry productivity across Inuit Nunangat (i.e., the Inuit territories of Canada).

## Materials and methods

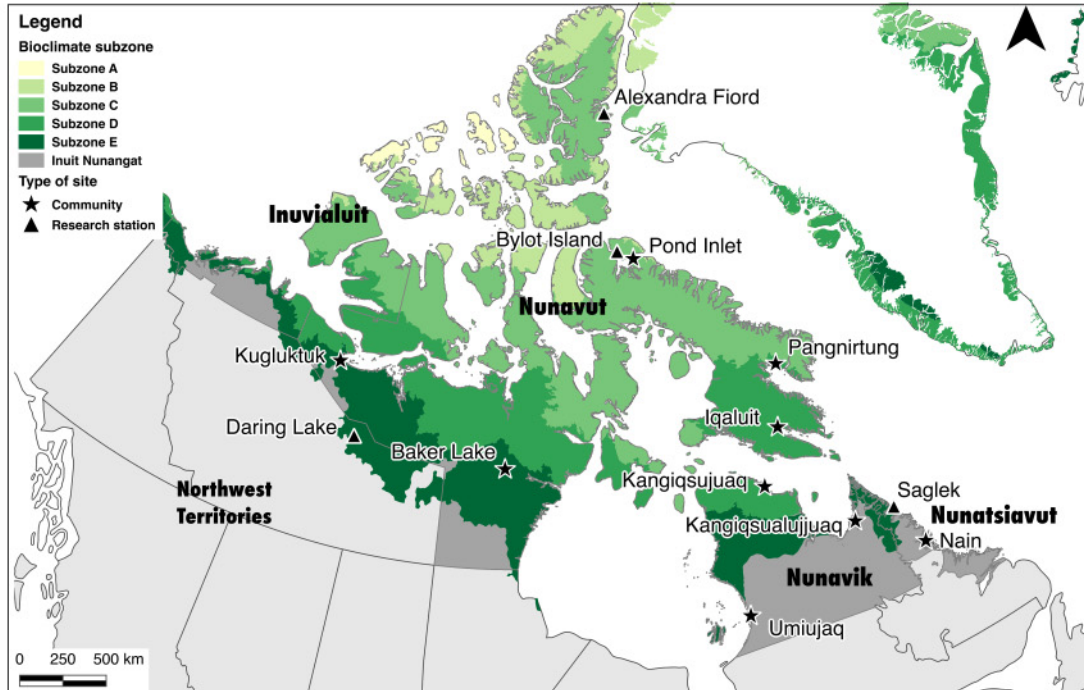
### Study sites

Berry-monitoring sites were established in three of the four regions of Inuit Nunangat in the vicinity of research stations and Inuit communities (Fig. 1). When possible, sites were established in collaboration with local communities, and partnerships with high schools and colleges were developed to integrate berry monitoring in science classes. The sites were chosen and established by researchers from the Université du Québec à Trois-Rivières, Québec, Memorial University, Newfoundland, and the University of British Columbia, British Columbia, Canada. Plots were chosen based on accessibility, minimum disturbance to local harvesting sites, and abundance of berries to reflect berry availability in productive patches. Study sites were established in Nunavut, Nunatsiavut (Newfoundland and Labrador), Nunavik (Quebec), and the Northwest Territories. Sites were located within or in close proximity to a vegetation subzone as defined by the Circumpolar Arctic Vegetation Map (CAVM: Walker et al. 2005). The CAVM subzones were good indicators of the dominant vegetation type at the study sites. Only prostrate vegetation (<15 cm) was found at Alexandra Fiord, Bylot Island, and Pond Inlet located in subzone C. Pangnirtung, Kangiqsujuaq, and Iqaluit are located in subzone D and vegetation is generally prostrate with low (>40 cm) shrubs growing in sheltered areas. Baker Lake, Daring Lake, Kugluktuk, and Saglek are located in subzone E where there is a mixture of low and tall (>2 m) shrub vegetation. Kangiqsualujuaq, Nain, and Umiujaq are located south of the tree line as delimited by the CAVM. Vegetation at these sites is characteristic of the transition from forest to tundra, hereafter referred to as the forest–tundra ecotone. A total of 37 study plots were established between 2008 and 2011, and analyses were performed on 31 of those plots for which productivity was documented during at least three growing seasons between 2008 and 2016 (Table 1).

### Study species

The study focused on the three most common and widespread berry species used by Inuit in the Canadian Arctic, namely crowberry (*E. nigrum*, Fig. 2a), cranberry (*V. vitis-idaea*, Fig. 2b) and blueberry (*V. uliginosum*, Fig. 2c). Species names follow the classification of the Flora of North America (Flora of North America Editorial Committee 1993+). All species

**Fig. 1.** Study sites located in three Inuit territories, Nunavut, Nunavik (QC) and Nunatsiavut (NL), and the Northwest Territories (Government of Canada 2017). The color gradient indicates the five bioclimate subzones (CAVM Team 2003). Markers of different shapes indicate the type of site, i.e., community or research station. Map created using QGIS software (QGIS Development Team 2016) and Canada cartographic boundary basemap (Government of Canada 2016).



**Table 1.** Establishment date of sites across the Canadian Arctic (Nu, Nunavut; Nt, Nunatsiavut; Nk, Nunavik; NWT, Northwest Territories), vegetation zone (i.e., bioclimate subzone C, D, or E, or forest-tundra ecotone (FT)), number of plots (20 m × 20 m) at each study site, number of years during which each site was visited between 2008 and 2016, and number of plots sampled at each site when it was visited.

Sites	Vegetation zone	Start year	Total No. of plots	No. of years visited	No. of plots sampled each year
Alexandra Fiord (Nu)	C	2011	3	5	3
Bylot Island (Nu)	C	2009	1	6	1
Pond Inlet (Nu)	C	2008	3	6	1-3
Pangnirtung (Nu)	D	2008	2	4	2
Iqaluit (Nu)	D	2009	1	7	1
Kangiqsujuaq (Nk)	D	2008	2	5	2
Baker Lake (Nu)	E	2009	4	5	1-4
Daring Lake (NWT)	E	2008	1	6	1
Kugluktuk (Nu)	E	2010	3	5	1-3
Saglek (Nt)	E	2008	6	3	1
Kangiqsualujuaq (Nk)	FT	2008	2	3	2
Umiujaq (Nk)	FT	2009	3	3	1-3
Nain (Nt)	FT	2009	6	3	6

Note: Only *Vaccinium uliginosum* was studied at Alexandra Fiord, Bylot Island, and Pond Inlet. All three study species were evaluated at the other sites. Study sites are presented following their order on the bioclimate gradient from highest to lowest.

Fig. 2. Study species: (a) *Empetrum nigrum*, (b) *Vaccinium vitis-idaea*, and (c) *Vaccinium uliginosum*.



are woody dwarf shrubs that belong to the Ericaceae family. They have a circumpolar distribution and range from the forest–tundra ecotone to the high Arctic in sheltered areas (Aiken et al. 2007); they are generally found in poor soil with higher C/N ratio (Heikkinen and Mäkipää 2010). *Empetrum nigrum* is a low (5–30 cm: Aiken et al. 2007) woody species with horizontal stems branching extensively to form a mat plant habit. 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). *Vaccinium vitis-idaea* is an evergreen species with small shiny oval leaves that produces white to pink flowers and spherical bright red fruits. It is often observed growing in well-drained to dry habitats. *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. Flowers are pink and bell-shaped; fruits are dark blue.

#### Field measurements

At each site, except Alexandra Fiord, at least one but up to six 20 m × 20 m plots were permanently marked (Table 1). The number of plots surveyed varied annually according to local participation and researchers' visits; overall between 14% and 57% of the plots were surveyed each year. Information on vascular plant species, moss, lichen, bare ground, and standing water cover was collected in each plot at the time of establishment using Braun-Blanquet cover classes (Braun-Blanquet 1932) or the point intercept method (Molau and Mølgaard 1996). Initial plot assessment also included a basic physical description (i.e., elevation, drainage, slope, and aspect). To help account for the heterogeneous distribution of berries, we aimed to record a minimum of 25 quadrats with berries. Randomly placed 25 cm × 25 cm quadrats were assessed until 25 quadrats with berries were found; quadrats with and without berries were used to calculate the average per plot. The number and fresh weight of berries were measured for each species separately in each quadrat. At Alexandra Fiord, berries were collected in a total of 30 permanent 25 cm × 25 cm quadrats located ca. 3 m apart along three randomly located transects ( $n = 10/\text{transect}$ ) within an area where *V. uliginosum* was common; the three permanent transects were considered as equivalent to plots at other sites. After fieldwork and laboratory analyses, data were sent to the affiliated university.

### Climate data

Climate data (i.e., all temperature data and 70% of precipitation data) were extracted from CANGRD, a gridded dataset with a 50 km resolution. In CANGRD, grids of monthly temperature and precipitation were generated through statistical interpolation using adjusted and homogenized climate data (AHCCD: [Environment Canada 2012](#)). AHCCD were systematically adjusted for instrument relocation, trace observations, and changes in observing procedures and are, therefore, the most reliable climate data for Canada. Precipitation data for Baker Lake, Iqaluit, and Pond Inlet were extracted directly from the Environment Canada website ([Environment Canada 2018](#)) due to large gaps in the AHCCD precipitation data for those sites.

### Statistical analyses

The berry productivity and vegetation cover data were used to conduct two main analyses. First, we evaluated the influence of plant species composition and local environmental factors on the abundance of berries, hereafter called the spatial analysis. Second, we modelled the inter-annual variation in the number and weight of berries across study sites in relation to climate, hereafter called the inter-annual analysis. All statistical analyses were conducted using the R statistical environment ([R Development Core Team 2016](#), version 3.3.1).

#### *Spatial analysis*

A non-metric multidimensional scaling (NMDS) ordination using the plant species data was computed to assess differences in vegetation composition among plots and sites. The plant species cover data measured with Braun-Blanquet classes were standardized to 100% cover for each quadrat, and then averaged per plot. For the point intercept data, the top hits were standardized to 100 total hits for each quadrat, and then averaged per plot. The analysis was performed using the metaMDS function in the R vegan package, version 2.4-1 ([Oksanen et al. 2012](#)). A three-dimensional ordination displayed the least stress and was repeated 100 times to reach the best solution for each NMDS ([Legendre and Legendre 1998](#)). The effect of local environmental factors (i.e., elevation, latitude, and cover of erect shrubs (>15 cm), lichens, and mosses) on the relative productivity of each berry species per plot (i.e., abundance of berries/species cover) was tested using a linear model. The difference in mean abundance of berries per species and bioclimate subzone was tested with a one-way analysis of variance (ANOVA) (R base package, function aov). A Tukey's honest significant differences was used to test multiple pairwise-comparison between subzones for each species (R base package, function TukeyHSD).

#### *Inter-annual analysis*

A generalized linear mixed model with normally distributed random effects was fitted using penalized quasi-likelihood estimation (package MASS, version 7.3-45, function glmmPQL: [Venables and Ripley 2002](#)). Even though the detailed berry abundance per quadrat was known, we used the average per plot to avoid an excess of zero counts, and because we were interested in inter-plot and inter-site variability. Based on similarities in vegetation, temperature, and precipitation, we conducted the analyses on three groups of sites: Group I, Alexandra Fiord, Bylot Island, and Pond Inlet; Group II, Baker Lake, Daring Lake, Iqaluit, Kangiqsujaq, Kugluktuk, and Pangnirtung; Group III, Kangiqsualujuaq, Nain, Saglek, and Umiujaq. The groups correlated strongly with their CAVM subzone: Group I sites were all in subzone C; Group II were all in subzones D and E; and Group III were all in the forest-tundra ecotone, except Saglek, which is in subzone E. A negative-binomial distribution was used for the abundance of berries (count data) and a Gamma distribution with a log link function was used for the weight of berries (continuous data).

To satisfy the requirements of the Gamma distribution, the analyses were performed on all weight values above zero. The abundance and weight of berries for each of the three species were tested against standardized climate variables (i.e., (variable( $t$ ) – average of variable)/standard deviation of variable) with plot and site as random effects. Based on the literature, the explanatory variables selected were: (1) mean June temperature, (2) total June precipitation, (3) mean temperature during July–August, (4) total precipitation during July–August, (5) mean temperature from November to April prior to the growing season, (6) total precipitation from November to April prior to the growing season, (7) mean temperature during July–August of the previous year, and (8) total precipitation during July–August of the previous year. These periods were selected as they are the best approximations of the growing season (July–August), dormant season (November–April), and transitional “spring” season (June) for the study area. The final models were selected following a backward selection method, i.e., the variables with the lowest fit were successively dropped. Models were validated by visual evaluation of the plotted response and deviance residuals (Zuur et al. 2009).

## Results

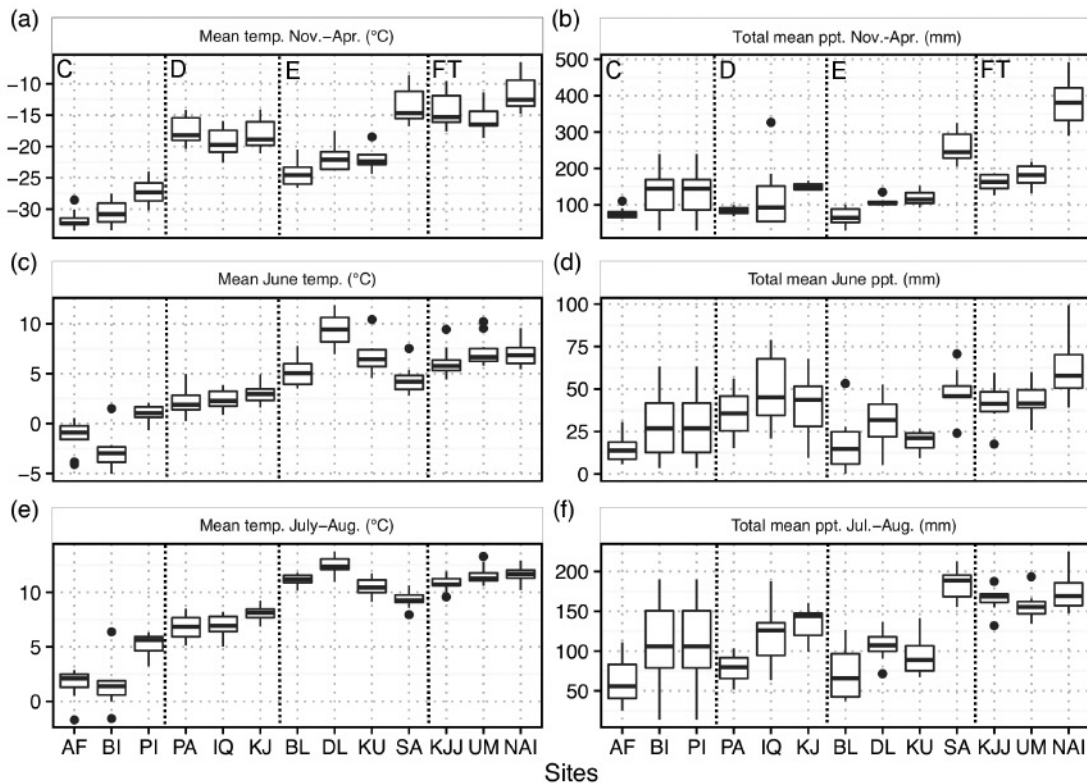
The data presented in this synthesis are spatially and temporally complex. The sites present a gradient in annual temperatures with mean temperature during July–August from 0.8 °C (Bylot Island) to 11.7 °C (Nain; Fig. 3). Precipitation in June and July–August also presents a clear gradient with a minimum during July–August of 32 mm at Alexandra Fiord and a maximum of 90 mm at Nain. In contrast, winter precipitation (November–April) was similar among sites (66–180 mm), with the exception of Saglek and Nain that received a greater amount of snow (260 and 380 mm, respectively). Since 2013, there has been a shift from human observations to automatic meteorological stations in the Canadian Arctic. The data collected using the new instrumentation have yet to be standardized and included in CANGRD, which accounts for the increasing number of missing precipitation data in recent years (E. Milewska, Government of Canada, personal communication, 2018).

The total abundance of fruits in subzone D (Pangnirtung, Iqaluit, and Kangiqsujaq) as well as in Saglek was higher than elsewhere, with the total abundance of all species estimated at 484, 370, 361 and 376 berries/m<sup>2</sup>, respectively (Fig. 4). Abundance at the other sites varied from 105 to 225 berries/m<sup>2</sup>. This corresponded to an average of 4.7–30.2 g/m<sup>2</sup> of *E. nigrum*, 0.40–36.30 g/m<sup>2</sup> of *V. uliginosum* and <0.01–14.08 g/m<sup>2</sup> of *V. vitis-idaea*. *Vaccinium uliginosum* was the only species collected in subzone C (Alexandra Fiord, Bylot Island, and Pond Inlet). At most sites outside of subzone C, *E. nigrum* was the species with the highest abundance of fruits. Average number of fruits per site is generally a good estimation of the abundance of berries in productive patches for those regions; however, sites where a small number of plots were sampled may be less representative (i.e., Bylot Island, Daring Lake, Iqaluit). Inter-annual variability was important at all sites and standard deviation per species and plot ranged from 1 to 240 berries/m<sup>2</sup>.

### Spatial analysis

NMDS ordinations showed differences among sites based on plant species cover (Fig. 5). Results present a gradient in vegetation from subzone C (i.e., Alexandra Fiord, Bylot Island, and Pond Inlet) at the far left to the forest–tundra ecotone (i.e., Kangiqsualujuaq, Nain, and Umiujaq) at the far right of the ordination. Sites in subzone C were markedly different in species composition, whereas there were more similarities among sites of subzone D (i.e., Iqaluit, Kangiqsujaq, and Pangnirtung), subzone E (i.e., Daring Lake, Kugluktuk, and Saglek), and the forest–tundra ecotone. All sites except Daring Lake associated more closely with sites from their respective bioclimate subzone. We obtained similar

**Fig. 3.** Climate data for all study sites and explanatory variables used in the model for the period 2007–2015: (a) Mean temperature from November to April (°C), (b) total mean precipitation from November to April (mm), (c) mean June temperature (°C), (d) total mean June precipitation (mm), (e) mean temperature during July and August (°C), and (f) total mean precipitation during July and August (mm). Study sites are presented following their order on the bioclimate gradient from highest to lowest latitude (Subzone C: AF, Alexandra Fiord; BI, Bylot Island; PI, Pond Inlet; Subzone D: PA, Pangnirtung; IQ, Iqaluit; KJ, Kangiqsujuaq; Subzone E: BL, Baker Lake; DL, Daring Lake; KU, Kugluktuk; SA, Saglek; Forest–tundra ecotone: KJJ, Kangiqsualujuaq; UM, Umiujaq; NAI, Nain). Note that the same precipitation data were used for Bylot Island and Pond Inlet.



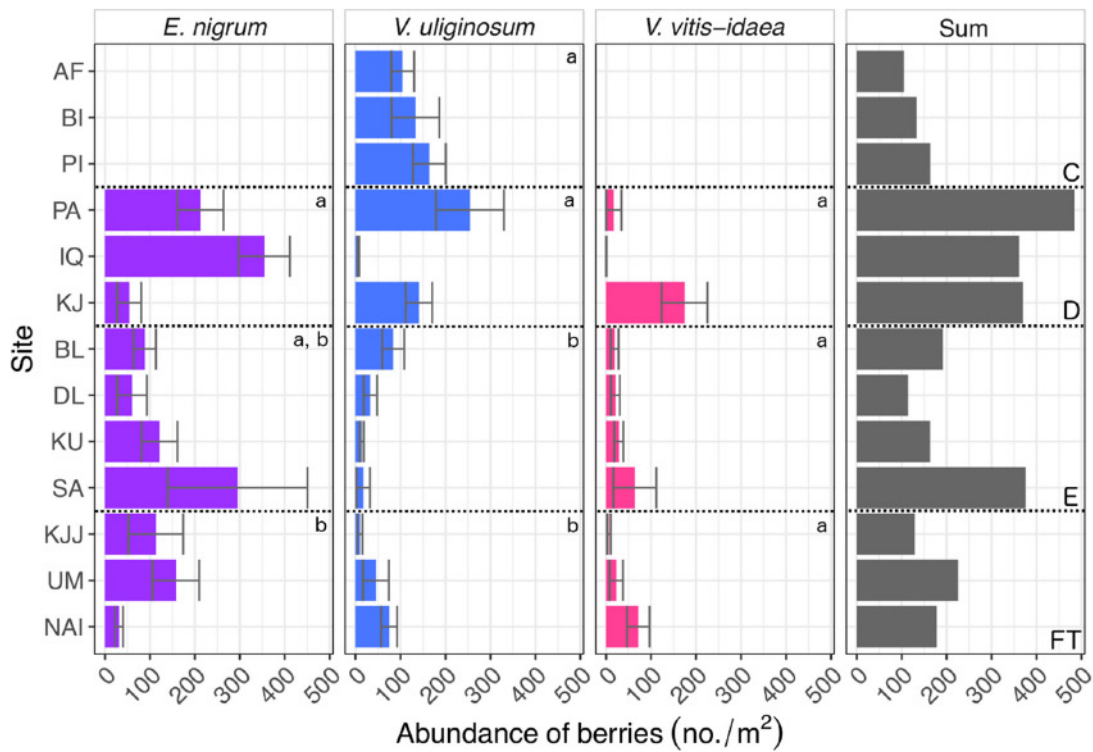
results when using the plot instead of the site as the grouping factor indicating that even though plots varied in their plant composition and environmental conditions, they are closely linked to their position along the climatic gradient. There was no significant correlation between the abundance of berries and the environmental variables tested (i.e., elevation, latitude, and cover of erect shrubs, lichens and mosses). The ANOVA identified significant ( $p < 0.05$ ) differences in mean berry abundance among subzones for *E. nigrum* and *V. uliginosum* but not *V. vitis-idaea*. For *E. nigrum*, Tukey's multiple pairwise-comparisons indicated a significant difference ( $p < 0.05$ ) in mean abundance of berries between subzone D and the forest–tundra ecotone, but not between subzones D and E nor between subzone E and the forest–tundra ecotone (Fig. 4). For *V. uliginosum*, there were no significant differences in abundance between subzones C and D and no differences between subzone E and the forest–tundra ecotone. However, abundances were significantly different between the two northern (C and D) and two southern subzones (E and forest–tundra) (Fig. 4).

#### Inter-annual analysis

The generalized linear models showed the contrasting effects of winter (November–April), spring (June) and summer (July–August) conditions on *V. uliginosum* berry



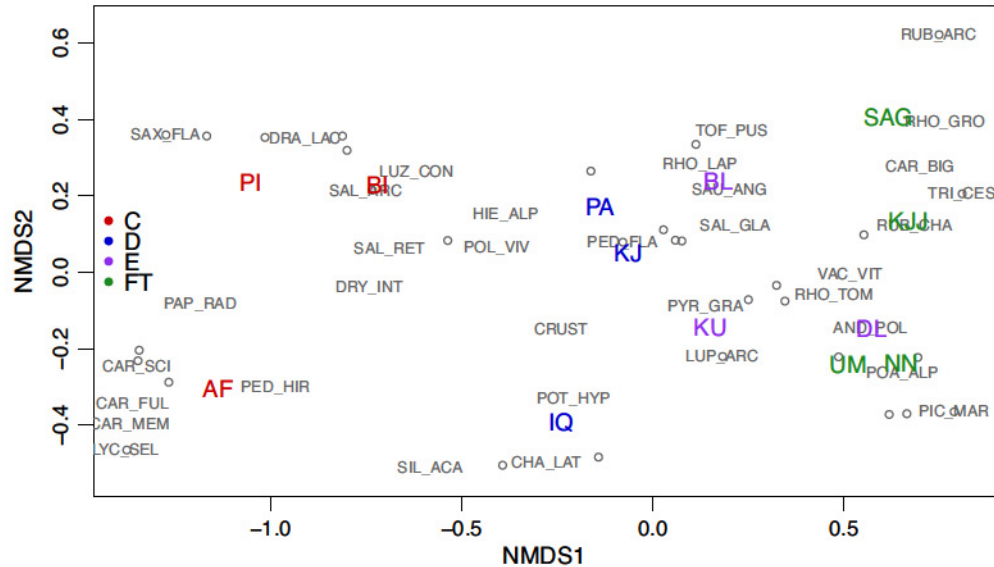
**Fig. 4.** Mean abundance (No./m<sup>2</sup>) and standard error of the three berry species at each study site between 2008 and 2015. Study sites are presented following their order on the bioclimate gradient from highest to lowest latitude (Subzone C: AF, Alexandra Fiord; BI, Bylot Island; PI, Pond Inlet; Subzone D: PA, Pangnirtung; IQ, Iqaluit; KJ, Kangiqsujuaq; Subzone E: BL, Baker Lake; DL, Daring Lake; KU, Kugluktuk; SA, Saglek; Forest–tundra ecotone: KJJ, Kangiqsualujuaq; UM, Umiujaq; NAI, Nain). Lowercase letters represent the results of the Tukey's honest significant differences test after analysis of variance (ANOVA) for each species where different letters indicate a significant ( $p < 0.05$ ) difference between subzones.



productivity in Groups I and II (Table 2). The small number of observations and missing precipitation data in Group III did not allow the completion of any significant models. None of the climate variables tested significantly influenced the berry productivity of *E. nigrum* berries in Group II and the species was not sampled in Group I. None of the models using the abundance and weight of *V. vitis-idaea* berries converged due to the small numbers of observations. In all models except those for *V. uliginosum*, abundance and weight of berries in Group II, the random effect “site” had a smaller slope than the random effect “plot”.

In the Group I sites, berry abundance of *V. uliginosum* was positively affected ( $p < 0.05$ ) by June temperature and July–August precipitation but negatively affected by November–April precipitation. The weight of *V. uliginosum* berries at sites in Group I was positively affected by July–August precipitation and July–August temperature of the previous year, but negatively affected by June precipitation. In the Group II sites, July–August temperatures positively influenced the abundance and weight of *V. uliginosum* berries and July–August precipitation in the previous year also negatively influenced the abundance of *V. uliginosum* berries.

**Fig. 5.** Results from non-metric multidimensional scaling (NMDS) ordination (stress = 0.06) using the plant species cover per site. The colour of each site name indicates its location along the bioclimate gradient (Subzone C: AF, Alexandra Fiord; BI, Bylot Island; PI, Pond Inlet; Subzone D: PA, Pangnirtung; IQ, Iqaluit; KJ, Kangiqsujuaq; Subzone E: BL, Baker Lake; DL, Daring Lake; KU, Kugluktuk; SA, Saglek; Forest-tundra ecotone: KJJ, Kangiqsualujjuq; UM, Umiujaq; NAI, Nain).



## Discussion

All berry pickers in the North have a hypothesis regarding the meteorological and environmental factors that make for a good berry year and a good berry patch. This knowledge is based on lifelong observations and Indigenous knowledge of climate and local environment impact on berry productivity in their local areas. In this study, measurements of berry productivity, climate, and local environment gave us some insight on the regional abundance of berries and the climate factors driving year-to-year productivity, although results also highlighted the complexity of this response.

### Regional patterns in species composition and berry productivity

Plots were selected based on the abundance of one or more of the three berry species and, thus, had overall similar dominant plant species composition across the study area. Consequently, the plant species analysis showed that plant composition in both plots and sites were closely associated with the bioclimate gradient. However, berry productivity did not follow such a predictable pattern, and in the majority of models we observed greater variability in productivity (i.e., number and weight of berries) among plots than among sites within a regional group. Analyses did not show any significant direct effect of local environmental variables on berry productivity probably due to the small number of variables measured and the relatively small range of variability of these variables. For example, as sites with high cover of erect shrubs were not selected, it was unlikely that we would directly measure an effect of erect shrub cover on berry productivity. Lussier (2016), who specifically studied the productivity of *E. nigrum* and *V. uliginosum* along a gradient of erect shrub cover in Umiujaq, found that the productivity of both species decreased under increasing erect shrub cover. In this study, we can only infer the effect of erect shrubs on berry productivity based on the spatial distribution of the most productive sites toward

**Table 2.** Results from the generalized linear mixed-effect models for the inter-annual analyses with *Vaccinium uliginosum* (VAUL) and *Empetrum nigrum* (EMNI) abundance and fresh weight of berries.

	June temperature. <sup>t</sup>	June temperature standard error	June precipitation. <sup>t</sup>	June precipitation standard error	July–August temperature. <sup>t</sup>	July–August temperature standard error	July–August precipitation. <sup>t</sup>	July–August precipitation standard error	November–April precipitation. <sup>t</sup>	November–April precipitation standard error	July–August temperature. <sup>t-1</sup>	July–August temperature standard error	July–August precipitation. <sup>t-1</sup>	July–August precipitation standard error	Site	Plot	df
<b>Group I</b>																	
VAUL (No.)	0.608	0.145	—	—	—	—	0.600	0.142	-0.475	0.135	—	—	—	—	<0.001	0.444	30
VAUL (g)	—	—	-1.109	0.331	—	—	0.442	0.191	—	—	1.373	0.253	—	—	<0.001	0.687	30
<b>Group II</b>																	
VAUL (No.)	—	—	—	—	0.590	0.160	—	—	—	—	—	—	-0.343	0.146	1.059	0.685	35
VAUL (g)	—	—	—	—	0.487	0.145	—	—	—	—	—	—	—	—	1.162	0.623	39
EMNI (No.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	<0.001	2.150	42
EMNI (g)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.373	0.493	32

Note: Only significant ( $p < 0.05$ ) slopes are shown with standard errors for variables associated to the year of observation ( $t$ ) and the year before observation ( $t-1$ ). Sites are classified as Group I: Alexandra Fiord, Bylot Island and Pond Inlet and Group II: Baker Lake, Daring Lake, Iqaluit, Kangiqsujuaq, Kugluktuk and Pangnirtung.

**Table 3.** Average berry productivity ( $\text{g/m}^2$ ) for *Empetrum nigrum*, *Vaccinium uliginosum*, and *V. vitis-idaea* in the boreal forest of Canada and Scandinavia as well as in the tundra of the Canadian Arctic (this study).

Species	Average productivity ( $\text{g/m}^2$ )		
	Boreal forest		Tundra
	Canada <sup>a</sup>	Scandinavia <sup>b</sup>	Canada
<i>E. nigrum</i>	0.04–2.04	NA	4.71–30.22
<i>V. uliginosum</i>	0.02–0.75	NA	0.40–36.30
<i>V. vitis-idaea</i>	0.52–3.49	0.3	<0.01–14.08

<sup>a</sup>Murray et al. (2005).

<sup>b</sup>Ihalainen et al. (2003).

the northern edge of species distribution range where erect shrubs are less abundant (i.e., subzones D and E for *E. nigrum*, and subzones C and D for *V. uliginosum*).

Although the data available in this study limit site specific interpretations, we suggest that it is in the northern ends of the species distribution range that berry productivity is the highest. This could be due to reductions in biotic interactions, such as shading by taller shrubs or other competitive effects, and environmental stressors (Svoboda and Henry 1987). This hypothesis is supported by the comparison with berry productivity data collected within the Gwich'in settlement areas located at the northern extent of the Canadian boreal forest (Murray et al. 2005) as well as in central Finland (Ihalainen et al. 2003). The difference is striking, with much higher productivity values found in this study for all three berry species (Table 3). Berry productivity data collected near Kluane Lake in Yukon (Krebs et al. 2009) also indicate that productivity for the three study species is higher in the tundra than in the boreal forest; however, results are not as directly comparable because of differences in field sampling methodology.

#### Impact of climate on berry productivity

A number of studies have focused on the impact of winter conditions on berries, as these are expected to experience major changes under current climate change scenarios (IPCC 2013). Northern residents usually associate a thick layer of snow with high berry productivity (Guyot et al. 2006; Cuerrier et al. 2015). In this study, we only found a negative impact of winter precipitation on the abundance of *V. uliginosum* berries at the northernmost sites (i.e., subzone C or Group I), likely because the growing season is already short at this end of the species distribution range and further shortening due to a long snowmelt period would decrease reproductive success. Moreover, in the high Arctic, *V. uliginosum* is largely found in moist soils where snow cover is persistent at the beginning of the growing season (Muc et al. 1989). Wipf and Rixen (2010), in a meta-analysis of experimental snow manipulation studies, found that the impact of snow cover on berry shrub growth and productivity was linked to the amplitude of change in snow depth as well as plant habitat (i.e., exposed with early snow melt vs late laying snow patches). The increase in winter precipitation recorded in the Arctic (up to 20% between 1950 and 1990: Groisman and Easterling 1994) has been associated with stronger winds modifying the distribution and quality of the snow (Gearheard et al. 2010; Gérin-Lajoie et al. 2016). Under these conditions, exposed sites may accumulate less snow, whereas sheltered areas would get additional snow. In areas where snow accumulates, the negative impact of delayed snowmelt would outweigh the benefits of a thick snow layer, such as protection from desiccation in winter and water input in spring (Wipf and Rixen 2010).

In this study, like in many others (e.g., Krebs et al. 2009; Selås et al. 2015; Boulanger-Lapointe et al. 2017) spring and summer conditions were most important to explain berry productivity. We did, however, detect differences in responses between high and low Arctic sites. For example, June precipitation only had a negative impact on productivity at high Arctic sites, likely because in that region precipitation in June often falls as snow. Moreover, the positive influence of June temperatures in the high Arctic may be associated with the sensitivity of pollination success to cold temperatures (Jacquemart and Thompson 1996). July–August precipitation also only had a positive impact in the high Arctic where sites are generally drier and more reliant on local sources of water (e.g., spring runoff and permanent snow patches). Overall, the variables important for productivity at high Arctic sites were closely associated with the onset of the growing season, such as June temperature and precipitation as well as winter precipitation, and water availability during the growing season, whereas those important at low Arctic sites reflected conditions during the growing season.

Previous studies of berry shrubs found a significant impact of the abundance of rodents on plant growth and reproduction (Laine and Henttonen 1983; Callaghan and Emanuelsson 1985; Boulanger-Lapointe et al. 2017) as well as the abundance of berries on rodent populations (Krebs et al. 2010; Selås et al. 2013). Local observations (Boulanger-Lapointe et al. 2019) and scientific investigations (Hupp et al. 2013) in the Arctic also indicated that geese may consume a large number of berries; however, not all study sites experienced goose herbivory. Even though the impact of berry consumption was mitigated by visiting plots before most berries were ripened; presence of scats containing berries near some of the plots indicated that animal consumption did in some instances occur before berry productivity values were recorded for this study. Moreover, early berry picking by local communities as well as herbivory on leaves and stems of the berry species may also have influenced our results and accounts at least partially for the unexplained variability in the models.

Although this study used the most extensive berry productivity dataset collected in the Canadian Arctic to date, the time-series examined were still relatively short (eight years) and it was not possible to test the impact of a greater number of variables such as conditions in May or in previous years due to a loss in statistical power when increasing the number of predictors (Howell 2011). This project showed that it is logistically challenging and costly to maintain a network of study sites in the Canadian Arctic without strong local partnerships, like the Arctic College in Iqaluit, the presence of a research station nearby (i.e., Alexandra Fiord, Bylot Island, Daring Lake, Nain, and Pond Inlet) or the commitment of a research group to a selected number of sites (Umiujaq and Saglek).

## Conclusion

This research provides a first overview of the berry production of *E.nigrum*, *V.uliginosum* and *V. vitis-idaea* in the vicinity of Inuit communities and research sites in Canada. We found that the vegetation of selected berry patches varied in their plant community composition following the large latitudinal gradient. Overall, the greatest berry productivity for the study species was observed toward the northern edge of their distribution range, perhaps due to a lessening of biotic interactions. Although the small number of observations limited the interpretation of the impact of climate on berry productivity, we found some interesting differences between high and low Arctic sites.

Our study demonstrates the widespread distribution and variability in production of northern berry shrubs and sheds light on some of the climate variables that may influence their productivity. The high annual variability may at least be partially attributed to the influence of local environmental factors and herbivory; however, there are likely other

important drivers of berry productivity and these should be further investigated to clarify some of the patterns observed in this study. Long-term monitoring and partnerships with Northern people and institutions will be key to gain a better understanding of the impacts of year-to-year fluctuations in climate as well as global climate change on berry productivity.

### Acknowledgements

Special thanks to all the undergraduate and graduate students, local field assistants and high school and college teachers and students who collected data for this study. We are grateful to the people who warmly hosted us in their home. Nicholas Coops, Susan Rowley, Jennifer Williams, and Amy Angert provided comments on an early version of the manuscript. This work was made possible by the logistical support of the Polar Continental Shelf Program (PCSP), Parks Canada and the Royal Canadian Mounted Police as well as the financial support of the Canadian International Polar Year program (IPY-CiCAT), ArcticNet, the Centre d'Études Nordiques, the Natural Sciences and Engineering Research Council of Canada (NSERC), the Northern Scientific Training Program (NSTP) and the W. Garfield Weston foundation. Research was conducted under Nunavut Wildlife Research permits from 2008 to 2015 and Nunavut Territorial Park use permits from 2012 to 2014.

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