CLIMATE CHANGE IMPACTS ON BERRY SHRUB PERFORMANCE IN TREELINE AND TUNDRA ECOSYSTEMS

by

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Abstract

Climate variability and warming are directly, indirectly and irrefutably driving widespread changes in global aquatic and terrestrial ecosystems, with disproportionate poleward impacts. Across Arctic treeline and tundra, understanding how current and future changes will negatively affect subsistence resources is critical to mitigating climate change impacts on Indigenous peoples and northern flora and fauna.

In this study, I looked to Inuit knowledge and western scientific approaches at local and regional scales across Inuit Nunangat (Inuit regions of Canada, including Nunavut, Nunavik, and Nunatsiavut) to explore and test the impacts of climate variability and warming on treeline and tundra berry species, which are critical resources in Arctic ecological and cultural systems. My central hypothesis, which is rooted in local, traditional and scientific knowledge, is that climate-driven expansion of tall-shrub canopies will negatively impact fruit production of dwarf berry shrubs.

Through mixed methods approaches, including participatory interviews, climate analyses, ecological surveys, and experimental warming at different spatial and temporal scales, this study identifies the fundamental role of local processes in driving and explaining changes in dwarf berry shrub growth (abundance and height) and fruit production (occurrence and abundance of fruit) in eastern Low Arctic and Sub-Arctic Canada. The results consistently demonstrate that growth and fruit production of truly prostrate berry shrubs (i.e. *Vaccinium vitis-idaea* and *Empetrum nigrum*) with limited phenotypic plasticity in height growth are most at risk from warming and tundra shrubification in comparison to berry shrubs with greater height growth plasticity (*V. uliginosum)* due to canopy impacts on local resources. With this knowledge, I anticipate that the boundaries between low and tall shrub tundra plant communities will be zones of significant change in berry resources. Local resource mapping, with a specific focus on these transition zones will be critical to identifying priority areas for berry resource conservation and active management to ensure future access to a sustainable source of these culturally important resources.

Keywords: dwarf berry shrubs, climate variability and warming, shrubification, treeline, tundra, eastern Low and Sub-Arctic Canada, Inuit Nunangat

For my village

Acknowledgments

When I first considered pursuing a doctoral degree, I believed that I could not "go the distance" if my project wasn't meaningful and impactful. What I didn't realize, was that the people who guided and supported me - my supervisory committee, family, and community members - made all the difference in producing meaningful and impactful research. These people were my source of motivation, and their support carried me through times of unanticipated adversity when I began this journey in May 2009.

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List of Abbreviations and Symbols

Symbol/Abbreviation	Meaning
°C	Degrees Celsius
Δ	Change in
±	Plus or minus
%	Percentage
=	Equal
<	Less than
>	Greater than
α	Alpha
Begl	*Betula glandulosa*
CI	Confidence Interval
cm	Centimetre
CRU-T3	Climate Research Unit temperature data
CTL	Control
D	D-statistic
DJF	December, January, February
df	Degrees of freedom
e.g.	For example
Emni	*Empetrum nigrum*
F	F-statistic
FDF	Frost day frequency
ha	Hectare
i.e.	Which means
JJA	June, July, August
km	Kilometre
LAI	Effective leaf area index
m	Metre
m2	Metre squared
Max.	Maximum
Min.	Minimum
mm	Millimetre
MRPP	Multi-response permutation procedure
n	Sample size
NMDS	Non-metric multi-dimensional scaling
OTC	Open-top warming chamber
P	Probability
PRE	Precipitation
r	Pearson’s correlation value
SD	Standard deviation
SE	Standard error
sp.	Unknown species
spp.	More than one species
T	T-statistic
TEK	Traditional ecological knowledge
TMP	Temperature
Vaul	*Vaccinium uliginosum*
Vavi	*Vaccinium vitis-idaea*
WDF	Wet day frequency

Chapter 1: General Introduction

1.1 Introduction and Thesis Outline

Indigenous peoples of the Arctic, along with western scientists, share a common need to understand the mechanisms driving the extraordinary changes and impacts being observed and experienced throughout the circumpolar Arctic (Merculieff et al. 2017). Predicting and mitigating negative ecosystem and human health outcomes will require a collaborative approach with insights and solutions from Indigenous and western scientific knowledge systems (Makondo and Thomas 2018).

Across the coastal Canadian Arctic, Inuit are observing and experiencing environmental changes linked to climate variability and warming that span all taxa and ecosystems, with profound effects on subsistence resources (Watt-Cloutier 2015; Gerin-Lajoie et al. 2016; Tyson et al. 2016). Within treeline and tundra plant communities, Inuit knowledge identifies increasing constraints on the access, availability and quality of plant-based resources such as berries (Downing and Cuerrier 2011, Cuerrier et al. 2015), which are believed to be threatened by increasingly warmer and drier weather, and competition from rapidly expanding upright deciduous shrubs (Boulanger-Lapointe et al. 2019). As Elder Verona Ittulak (Nain) reported, “Those shrubs, avaalaKiak (Arctic dwarf birch), are affecting berries quite a bit because you know the berry leaves, they are being covered by those things. [...] less berries now maybe because of those avaalaKiak” (Chapter 2). However, not all berry species perform equally in response to changing climate; predicting how individual berry species will respond to climate variability, fluctuating resource availability, and shifting species’ interactions will require a well-rounded understanding of tundra resource gradients, variations in species' traits, and their responsiveness or resilience to shifting ecological pressures (Wookey 2008).

My objective throughout this thesis was to advance our understanding of how tundra berry plants respond to climate variability and warming at different spatial and temporal scales, to better support land-use planning and climate change adaptation initiatives across Inuit Nunangat (Inuit regions of Canada). Recognizing the complexity in predicting changes in tundra berry resources, I utilized a mixed-method approach based on Inuit knowledge, climatological records, ecological surveys and in-situ field experiments. This study makes an important contribution to the climate change literature by incorporating multi-region, -site, -species, and -year approaches that fill an existing knowledge gap on the future availability and viability of tundra berry resources.

In Chapter 2, *Local assessments of environmental change in Arctic Canada: an integrated approach to analyzing Inuit observations and climate data*, we explore geographic patterns in Inuit observations of environmental changes from eight Canadian Arctic communities spanning three Inuit regions of Canada and compare these patterns to 30-year trends in local climate variability. Given the geographic coverage of Inuit knowledge in this study and the use of a new analytical approach, we were able to generate important insights on the scope and extent of climate change impacts (including berries) and potential drivers of change.

Chapter 3, *Strong canopy-understory feedbacks on fruit production at treeline*, returns to classical ecological surveys across abiotic and biotic gradients to determine canopy-understory feedbacks on the performance of three dwarf berry shrubs. This paper validates the prediction that expansion of tree and tall-shrub canopies can reduce fruit production and availability among low shrub tundra ecosystems.

Chapters 4 and 5 test the relationship between three dwarf berry shrubs and upright deciduous shrubs using experimental warming, over a 2- and 3-year period in eastern Sub- and Low-Arctic Canada, and over a six-year period in eastern Sub-Arctic Labrador. In Chapter 4, *Experimental warming effects on performance of culturally significant dwarf berry shrubs in eastern Low- and Sub-Arctic Canada*, our multi-species, multi-site approach demonstrated the widespread responsiveness of upright deciduous shrubs to warming and is among the first to identify divergent responses among prostrate or low-growing berry shrubs. Chapter 5, *Fruit production decreases among culturally important prostrate berry shrubs following seven years of experimental warming in Sub-Arctic Labrador, Canada*, builds on our understanding from Chapter 4 by demonstrating phenotypic responses to changing resource availability among berry shrubs over a longer time period, a gradient in impacts on prostrate vs. upright berry shrubs, and that truly prostrate berry shrubs are most vulnerable to tundra shrubification.

1.2 Co-authorship Statement

This research was conducted independently under the supervision of Dr. Luise Hermanutz. For Chapters 3 and 5, I was responsible for experimental design, collection of data and sample processing, statistical analysis and writing the manuscripts. Data collection in the field was assisted by Daniel Myers, Anita Kora, Elias Obed, James Wall, Allison Ford, Darroch Whitaker, Rodd Laing, Alain Cuerrier and Luise Hermanutz.

Chapter 3 is co-authored by Luise Hermanutz, and Chapter 5 by Luise Hermanutz and Alain Cuerrier.

Chapters 2 and 4 are syntheses chapters whereby co-authors contributed data from different regions across the Canadian Arctic. In Chapter 2, co-authors contributed qualitative data based on interviews from Nunavut and Nunavik. For Nunatsiavut, I developed, conducted and transcribed interviews. Co-author Alain Cuerrier was present to oversee my interview process in Nain, Nunatsiavut. I was then responsible for harvesting quantitative data for all regions, data collation, building multi-site datasets, statistical analysis and writing the manuscript. This chapter is co-authored by Jose Gérin-Lajoie, Alain Cuerrier, Luise Hermanutz, Esther Lévesque, Carmen Spiech and Greg Henry. In Chapter 4 I was responsible for experimental design and data collection at two experimental warming sites in Nunatsiavut. Co-authors contributed data from three sites in Nunavik. I was responsible for data collation and standardization, building quantitative datasets, analysing the data and writing the manuscript. Co-authors on this chapter include Luise Hermanutz, Alain Cuerrier, Charlene Lavalée and Esther Lévesque.

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1.4. Permits and Licences

The interview protocol and semi-structured questionnaire utilized in Chapter 2 followed the ethical guidelines with full permission from participants under ethics permits obtained by Université du Québec à Trois-Rivières for Nunavik (#CER-07-124-07.18), Memorial University of Newfoundland (ICEHR2008/09-131-SC), Nunavut Research Institute (Permit #05 070 11R-M), and Nunatsiavut Government Research Advisory Committee (June 2009).

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Chapter 2: Local assessments of environmental change in Arctic Canada: an integrated approach to analyzing Inuit observations and climate data

Siegwart Collier, L., J. Gérin-Lajoie, A. Cuerrier, L. Hermanutz, E. Lévesque, C. Spiech, and G. Henry

Abstract

The Arctic is experiencing unprecedented environmental changes linked to increased temperatures, climate variability, population growth and development. Understanding how these changes compare across northern communities and regions is essential for effective resource management, mitigation and adaptation response. Here, we explore geographic patterns in Inuit observations of environmental changes from eight Canadian Arctic communities spanning three Inuit regions of Canada and compare these patterns to 30-year trends in local climate variability. Qualitative and quantitative data were combined using multivariate ordination [non-metric multidimensional scaling (NMDS)] to 1) generate new insights on climate change impacts across the Canadian Arctic, their scope, and potential change drivers, and 2) to test a new methodology for evaluating such change. Our trend analysis supported strong local controls on climate variability among communities. Ordination combined Inuit observations on multiple environmental variables with climate trend analyses over a large geographic area. Using this approach, we detected pan-Canadian Arctic patterns of change in the timing of seasons, snowfall abundance, timing of sea-ice formation/break-up, and shrub abundance, and several regional patterns in weather and animal abundance. Several regional-scale patterns correlated with increasing precipitation over the 30-year period, including rainfall and animal abundance and changing sea-ice conditions. We also detected strong local patterns in tree and berry abundance. Greater inference on potential drivers of observed patterns could be realized through inclusion of local ecological and social factors, which may vary substantially among communities.

Keywords: Inuit observations of environmental change, Inuit regions of Canada, 30-year climate trends, multivariate ordination

2.1 Introduction

The combined effects of increased climate variability and warming, population growth and modernization have resulted in widespread environmental changes throughout the global Arctic. Ecosystem-level impacts include changes in plant species composition, abundance and distribution (Pouliot et al. 2008, Elmendorf et al. 2011, Henry et al. 2012, Pearson et al. 2013), widespread permafrost thaw (Hinzman et al. 2005, Lawrence et al. 2008, Way and Lewkowicz 2018), and shifts in terrestrial and marine mammal distribution (Kovacs et al. 2011, Côté et al. 2012). The speed and extent of these environmental changes is having a disproportionate and net-negative effect on northern Indigenous communities by changing access and availability to key natural resources that support local livelihoods, culture and traditions (Trainor et al. 2007, Buijs 2010, Downing and Cuerrier 2011, Mustonen 2013).

In response to the widespread changes occurring across terrestrial ecosystems and across Inuit Nunangat, a major research effort was undertaken as part of International Polar Year (2007-2008), and further supported through ArcticNet (2009-2019+), to understand the local and regional impacts of climate variability and warming on tundra vegetation, and how changes in tundra resources are affecting Inuit communities across Inuit regions of Canada (Henry et al. 2012). An overarching strategy within this research program was to collaborate with Inuit communities and governments to conduct community-based participatory (community-based monitoring, consultations and interviews), and standard scientific research (remote sensing, climate monitoring, vegetation surveys and in-situ experiments), to understand the complexity of terrestrial climate change impacts, and support appropriate and relevant adaptation response strategies that meet the needs and priorities of Canadian Arctic communities (Riedlinger and Berkes 2001, Berkes et al. 2007). In this chapter, we present one sub-project within this broader research program, which draws on local Inuit traditional ecological knowledge (TEK) documented through community interviews to 1) explore geographic patterns in Inuit observations of environmental changes from eight Canadian Arctic communities spanning three Inuit regions of Canada, and to 2) compare patterns in Inuit observations alongside 30-year trends in instrumental climate records. Here, Inuit TEK is presented as first-hand or lived observations of environmental change (Houde 2007). Inuit have an intimate connection with the environment developed through generations of living off the land and sea (Gearheard et al. 2010). This relationship, which is based on continual observation, intimate interaction with the environment and inter-generational knowledge transfer, gives rise to Inuit traditional ecological knowledge (TEK) (Huntington 1998). Lived observations, which represent only one of many facets of TEK (Houde 2007), are generated through the lens of Inuit culture and values [Inuit Qaujimajatuqangit – see Wenzel (2004)], and are an essential part of Inuit TEK as a whole.

Efforts to link northern Indigenous and scientific knowledge in the context of climate change generally fall into four broad groupings, often based on research from one or few communities within a region. Areas of research include:

- Identifying complementarities and differences between knowledge systems (Alexander et al. 2011, Evering 2012)

- Improving understanding of primarily community-specific changes in weather, wildlife and the physical environment (Krupnik and Jolly (editors) 2002, Laidler 2006, Gearheard et al. 2010, Weatherhead et al. 2010, Royer et al. 2013)
- Assessing implications of climate variability on community health, security and vulnerability (Ford et al. 2006, Furgal and Seguin 2006, Laidler et al. 2009, Cunsolo Willox et al. 2012)
- Building policy and strategies for adaptation response planning (Ford et al. 2010, Ford and Pearce 2012).

We make an important contribution to this body of literature in several key areas. First, this study is uniquely broad in geographic scope, incorporating and sharing Inuit TEK from eight Canadian Arctic communities across three Inuit regions of Canada. It also incorporates observations on multiple environmental variables that are inclusive of but not limited to subsistence harvesting. Lastly, this study explores a mixed-method approach to linking Inuit knowledge with climatological records using an analysis procedure (multivariate ordination) rooted in community and ecosystem ecology, to explore geographic patterns in assemblages of observations among Inuit communities. Collectively, this study aligns with the National Inuit Climate Change Strategy (Inuit Tapiriit Kanatami 2019) by conducting collaborative research in priority areas with potential contributions to policy at multiple jurisdictional scales.

Quantitative analysis of traditional knowledge is paradoxical in that grouping, coding or enumerating knowledge (a western scientific approach) can detach local and Indigenous knowledge from the rich and complex context in which it is situated (GNWT 2005, ITK and NRI 2006). In this study, a semi-structured approach was adopted to facilitate quantitative analysis; however, for each response the interviews also generated detailed narratives that placed participant responses within their lived context. These narratives were compiled to produce a multi-dialect book entitled *"The caribou taste different now" Inuit Elders Observe Climate Change* (Gerin-Lajoie et al. 2016), which documents the depth and richness of Inuit knowledge shared in this study while providing a means for communities across the Canadian Arctic to share their experiences with climate change, and to pass that knowledge on to future generations. We directly draw on narratives from this book to contextualize our quantitative results and frame our discussion. The mixed method approach presented in this study does not attempt to corroborate Inuit observations with instrumental climate records. Rather, we bring both knowledge sources together to:

1. Generate new insights on climate change impacts, their scope and potential drivers of change based on Inuit observations and climate trend analyses across the Canadian Arctic
2. Evaluate the spatial scale and consistency of climate change impacts
3. Test a new analysis procedure for exploring patterns among assemblages of Inuit observations and instrumental climate data, while examining the benefits and risks of this analytical approach

2.2 Methods

2.2.1 Study Sites

From 2007-2010, we conducted 144 interviews in eight communities spanning three Inuit regions of Canada (Fig. 2.1), including:

- Nunavut: Kugluktuk (17), Baker Lake (24), Pangnirtung (19), and Pond Inlet (15)
- Nunavik: Umiujaq (20), Kangiqsujuaq (17), and Kangiqsualujjuaq (9)
- Nunatsiavut: Nain (23)

Communities span approximately 16° latitude, with representatives from Sub- (Umiujaq, Kangiqsualujjuaq and Nain), Low- (Kugluktuk, Baker Lake and Kangiqsujuaq), Mid- (Pangnirtung) and High Arctic (Pond Inlet) Canada. As latitude increases, permafrost shifts from discontinuous to continuous, and vegetation from forest-tundra to tundra (Table 2.1). Local climate also varies with topography and proximity to marine environments. All communities apart from Baker Lake are coastal.

2.2.2 Study design

To investigate geographic patterns of change for multiple environmental variables, interviews were open to all community members with historic and current knowledge of the local environment. We used snowball sampling (Goodman 1961) initiated through local information sessions and advertising (radio and poster) (Appendix 2.1) in conjunction with purposive sampling (Tongco 2007), based on the recommendations of local governments, agencies, and interpreters. Collectively, this resulted in 144 core interviews with 88 women and 56 men, who ranged in age from 44-92 years. Core interviews ranged from 1-2 hours in duration, and in many cases, complementary mapping interviews were conducted to identify site-specific changes in natural and cultural resources throughout the respective regions. Participants self-identified as having spent considerable time on the land; either ongoing or in the past as in the case of some Elders. Many participants lived through government amalgamation and centralization of their ancestral communities, which generally occurred from 1930-1970 across Canada (Billson 2001). Therefore, we only included observations specific to their current community of residence. Most participants shared observations in the context of personal/family subsistence and cultural practices; however, some shared knowledge and observations acquired through their occupation, such as harvesters and environmental monitors.

Prior to interviews, individuals were informed of the project goals and research process, and their right to withdraw from the interview and/or research process either by notifying the interviewer or interpreter. Although participants had the option to withdraw at any point throughout the process, opportunities to personally connect with the research group and/or interpreter became fewer at the point of statistical analyses and writing. Participants were also made aware that they were free to respond to any/all questions for which they felt comfortable, or those of interest to them. Oral and/or written consent was obtained from each participant, in which they also specified how they wanted the interview to be documented (audio, video and/or manual recording of responses). Our interview protocol and semi-structured questionnaire followed the ethical guidelines with full permission from participants under ethics permits obtained by Université du Québec à Trois-Rivières for Nunavik (#CER-07-124-07.18), Memorial University of Newfoundland (ICEHR2008/09-131-SC), Nunavut Research Institute (Permit #05 070 11R-M), and Nunatsiavut Government Research Advisory Committee (June 2009).

Working with local interpreters, members of our research team interviewed participants primarily in the local Inuktut dialect, and occasionally in English. During a typical interview, the interviewer(s) would begin by requesting information on location and date of birth, and would use a semi-structured questionnaire (Appendix 2.2) accompanied by photographs and maps of each region (Huntington 1998) to cover the following themes: 1) berries and berry picking activities, 2) abundance, distribution, and use of plants, 3) influence of climate on plants, 4) changes related to animals and 5) human factors related to climate change (see Cuerrier et al. 2015 for details). Following the interviews, topics were broadly re-categorized, and included the following variables:

1) Weather/physical factors: timing of seasons, way of life (traditional practices), lake/sea-ice freeze and break-up; abundance of snow and rain; changes in snowmelt, temperature, permafrost, erosion, hydrology, lake/sea-ice thickness; variability in weather (total variables = 30)
2) Vegetation and berries: timing of bloom, abundance of all plants, trees, shrubs, grasses, mosses, lichens and berry plants; timing of berry ripening and taste; berry species included: *Rubus chamemorus* L. (cloudberry), *Empetrum nigrum* L. (crowberry/blackberry), *Vaccinium uliginosum* L. (blueberry), and *V. vitis-idaea* L. (mountain cranberry/redberry/lingonberry) (total variables = 35)
3) Animals: abundance and phenology of insects, mammals, fish and birds (total variables = 12)

2.2.3 Data summary and analysis

Community Interviews

We asked participants close-ended questions to objectively obtain quantitative responses on observed environmental changes. For example, "Have you observed changes in plant abundance?” Participants responded, “Yes or No”, and where appropriate, indicated the direction of change with context and examples (e.g. more/less). Participants understood “change” to be environmentally driven rather than anthropogenic (e.g. development, harvesting, pollution) and outside the natural rhythm of what is normal or expected for that area. Participants had the time and space to speak freely providing as much detail and context as they wished regarding their observations and experiences. This approach simultaneously generated detailed narratives relating to many aspects of Inuit TEK. For all communities, the temporal scale of observations occurred over the past 5-25 years with a median value of 10 years.

Following transcription of interview audio and notes, we quantified participant responses using binary (1=change; 0=no change) and ordinal (e.g. -1=less; 0=no change; 1=more) classification. Ordinal responses were separated into two binary variables [e.g. plant less (1=yes; 0=no), plants more (1=yes; 0=no)] to achieve a uniform binary response matrix. In the uncommon occurrences where a person did not know or chose not to answer, we attributed a 0-value, as for no observation of change. The proportion of observed change to no observed change (1’s to 0’s) was calculated for all variables within each community. Proportions were then pooled by interview category and presented as boxplots to summarize the frequency of observed change within communities for each interview category.

Results of our work were brought back to all communities for vetting through personal contact with participants and local governments. In many communities, results were shared at community open houses and through community-based publications such as bulletins and posters (Appendix 2.3).

Local climate analysis

We conducted trend analyses on a series of climate variables to investigate recent and local environmental changes for each community. As participants ranged from 44-92 years of age, we chose a 30-year period (1977-2007) in which participants were adults that overlapped with the general time frame of observed environmental changes (10-year median). Our intention was to use local climate station data available through Environment Canada's local weather station network (http://climate.weather.gc.ca/index_e.html); however data archives for each community varied greatly in length and completeness. This is especially pronounced among Nunavik communities, which have incomplete/missing data before 1992. As an alternative, we extracted monthly mean high resolution (0.5 x 0.5 degree) gridded climate data available for our period of interest for each community [Climatic Research Unit Time-Series 3.1 (CRU TS3.1), University of East Anglia CRU, 2011]. Monthly temperature (TMP) and precipitation (PRE) data were used to calculate mean annual temperature, total annual precipitation and mean temperature/total precipitation for the following seasonal periods: spring (April-May), summer (June-September), fall (October-November) and winter (December-March). We also calculated mean annual wet day frequency (WDF; days with precipitation) and frost day frequency (FDF; days with air temperatures <0ºC) for the period of 1977-2007 for each community. To investigate how accurately the gridded data represent local climate conditions for each community, we derived the same suite of climate variables using local station data for available time periods, and calculated the correlation coefficients between gridded and locally-derived variables (Appendix 2.4). We found strong and significant correlations between local and gridded data, supporting the use of gridded data in this study. Missing local station values contributed to weak correlation coefficients for mid and high Arctic communities.

To investigate the magnitude and significance of linear trends in climate variables for the period of 1977-2007, we estimated Theil-Sen slopes and 95% confidence intervals described by Yue et al. (2002) and implemented in Royer et al. (2013). This approach is suitable for time series without distributional assumptions, and accounts for lag-1 serial autocorrelation, which is common with climate data. We tested for significance ($p < 0.05$) using the non-parametric Mann-Kendall test (Helsel and Hirsch 2002). Trend analyses were performed in R (v2.15.3; R Development Core Team 2009) using the 'zyp' package (Bronaugh and Werner 2013). Analysis code can be found in Appendix 2.5.

Combining analysis of community interviews with local climate trends

We conducted multi-response permutation (randomization) procedures (MRPP) to test for statistical differences in participant observations among communities and between men and women, and we explored patterns and differences in assemblages of Inuit observations using non-metric multidimensional scaling (NMDS) ordination. Both procedures are highly suitable to community-based data, as neither relies on a random sample of the population (McCune and Grace 2002). NMDS is an indirect, non-parametric ordination technique that uses an iterative procedure to group similar data points or observations from large complex datasets to visualize and interpret patterns (McCune and Grace 2002). The approach makes few assumptions about the data distributions, which makes it highly flexible and an important distinction from traditional hypothesis-testing procedures (Legendre and Legendre 1998).

Ordinations were performed on untransformed data matrices (no significant outliers detected or removed), and we followed procedures outlined in Peck (2010) to specify initial analysis criteria (max. # axes = 4, max. # of iterations = 200, random starting coordinates, step length = 0.20, time = random # seed, 50 runs with real and randomized data) and to determine a final ordination solution. We chose Euclidean distance to calculate axes scores for MRPP and NMDS because our binary characters (0=absence of change; 1=presence of change) convey equal meaning for all categories of our questionnaire (Peck 2010). The MRPP and NMDS analyses were run individually for each questionnaire category using PC-ORD version 6 (PCORD v.6; McCune and Grace 2002).

Since the test statistics from our trend analyses (Kendall's tau) represent normalized values of the magnitude and direction of change for each time series, we overlaid these values as climate vectors in each NMDS ordination. This approach enabled us to equally explore relationships between interview responses and climate variables across sites. Pearson product moment correlation coefficients (r-values) were then used to interpret the strength and direction of relationships between interview responses/climate variables and ordination axes. With a large sample size, statistical significance is achieved with considerably low critical r-values (i.e. n=100, $p<0.05$ at r=0.197; Upton and Cook (2008). Therefore we chose a conservative cut-off value of "r" (|0.400|) to interpret statistically important relationships as suggested by McCune and Grace (2002).

To explore the context and implications of our ordination results, we draw on participant narratives and present select quotations alongside NMDS results. Many of these quotations are compiled and published in Gerin-Lajoie et al. (2016).

2.3 Results

2.3.1 Local climate trends

We found 30% of climate variables analysed from the gridded climate data showed significant changes over the 30-year period (Table 2.2). Apart from Pangnirtung, all communities showed general trends towards increasing annual temperatures. The magnitude of change for each community over the 30-year period was relatively small (<0.1°C/year), however, 4 of 8 time series demonstrated significant increases in annual warming with cumulative values ranging from ~1.5 to 2.5 °C over the 30-year period. Warming was most pronounced at Baker Lake, where we found significant warming trends annually and within each season. We detected a similarly widespread trend towards increasing fall temperatures across communities, apart from Kugluktuk and Pangnirtung. All communities, except Pangnirtung and Nain, showed general trends towards decreasing annual frost day frequency, however only half of these trends were significant. Kugluktuk, Pangnirtung and Kangiqsujuaq showed significant declines in annual wet day frequency. For most of the eastern communities (excluding Pangnirtung and Kangiqsujuaq), we found a general trend towards increased annual precipitation (1.16-4.79 mm/year), but only Kangiqsualujjuaq was significant. Pangnirtung was the only community with decreasing 30-year trends in temperature and precipitation; however, we also found small yet significant increases in winter precipitation (0.14 mm/year). While there was no apparent north-south or west-east gradient in rates of change, the direction of change for nearly all climate variables was consistent between western and mid-Arctic communities, and among all eastern communities.

2.3.2 Variation in Inuit observations and their correlation with climate trends

Higher median values in Panel A of Fig 2.2. indicate that environmental change was most frequently observed for variables regarding weather/physical factors, followed by animals (Panel C) and vegetation/berries (Panel B). Although more change was observed for weather/physical factors, tighter limits on the upper and lower ranges around the median indicate that response consistency was highest for variables regarding vegetation/berries (Panel B), followed by animals and weather/physical factors (Panel C, A). Responses within Pangnirtung, Pond Inlet and Kangiqsujuaq appeared to be the most consistent across all interview categories (Fig. 2.2).

Inuit observations were significantly different among communities for all questionnaire categories (Weather/physical factors: $T = -28.405$, $p < 0.001$; Vegetation/berries: $T = -31.245$, $p < 0.001$; Animals: $T = -13.730$, $p < 0.001$; Table 2.3), and for nearly all pairwise community comparisons across interview categories (Table 2.4), indicating the importance of local context in observations of change. Observations also differed significantly between men and women, but only regarding Weather/physical factors ($T = -2.777$, $p = 0.015$; Table 2.3).

All ordinations resulted in 3-dimensional solutions, however only the strongest two axes, environmental variables and climate vectors with r-values that met the critical cut-off ($r = |0.400|$) were plotted in Fig. 2.3a-c. A complete list of r-values for all environmental variables and climate vectors is provided in Table 2.5 and Table 2.6

respectively. To substantiate our interpretation of Fig. 2.3a-c, we provide scatterplots of interview responses against first and second ordination axes for each environmental variable that met our critical cut-off value (Peck 2010) (Appendix 2.6).

Weather and physical factors

The first two axes of the ordination for weather/physical factors (Fig. 2.3a) accounted for 31.9% and 24.4% of the variance explained (VE), respectively. Although consistency varied within communities (Fig. 2.2), there were strong relationships between “season” variables and axis 1, suggesting that the timing of seasons has changed for some communities (Winter: r = -0.658; Summer: r = -0.577; Fall: r = -0.514; Spring: r = -0.470). As one participant from Pangnirtung described, “Winter doesn’t usually come in until December. Back then it was November” – Evee Anilniliak, (pg. 170). Other important correlations along axis 1 included less snow (r = 0.563) and changes to wind (r = -0.409), which was reported by most participants from nearly all communities. Later sea-ice freeze up (r = -0.522) was also observed by all coastal communities, but to a lesser extent in Umiujaq and Pond Inlet. We observed an important relationship with axis 1 that traditional travel routes have changed (r = -0.538), influenced by strong agreement among eastern Sub/Low and High Arctic communities (especially Nain and Kangiqsujuaq). Some participants also indicated that temperature is colder now (r = -0.487). This correlation was strongly influenced by responses from Nain. An important contrast along axis 2 was that nearly all participants from Kugluktuk and the majority from Baker Lake were observing less rain throughout the year (r = -0.578), whereas communities in eastern Sub/Low Arctic (especially Nain and Kangiqsujuaq) were observing more rain (r = 0.469), in particular greater intensity of rainfall but similar frequency. From Kugluktuk, one Elder explained that “The rivers and lakes are drying up. Hardly any water left. Even Bloody Falls, where the river flows, we noticed the flow getting weaker. It’s getting less and less every year” – Lena Allukpik (pg. 59).

Correlations with axis 2, which were strongly influenced by responses from High Arctic and eastern Sub-Arctic communities, showed participants were observing earlier sea-ice break-up (r = 0.622) and thinner sea-ice conditions (r = 0.636; exceptions are Pangnirtung and Umiujaq). Participants from Nain and Kangiqsujuaq were also observing thinner lake ice conditions (r = 0.423). Participant responses on traditional practices or “Way of Life” from eastern communities were significant along both ordination axes (axis 1, r = -0.437; axis 2, r = 0.426). From Pangnirtung, one Elder explains that “As Inuit, our way of thinking has a lot to do with our environment. For people in the North, you know how the seasons work and your body has to be in sync with the land all the time. It’s true that your mind and body are not so much in sync with the land anymore.” – Jaco Ishulutaq (pg. 185). Correlations with axis 2 for rainfall and sea-ice conditions are similar to those for climatic vectors indicating increasing fall (r = 0.528) and annual (r = 0.449) precipitation (Fig. 2.3a).

Although the MRPP indicated that responses differed based on gender for weather/physical factors, when ordinations and individual scatterplots were grouped by gender (data not presented) there were no discernable patterns between males and females for individual variables.

Vegetation and berries

Ordination results regarding vegetation and berries (Fig. 2.3b) showed that axes 1 and 2 accounted for 53.7% and 22.3% of VE, respectively. Overall high VE was attributed to the observation (along axis 1) that berry abundance has declined (r = -0.800), especially for cloudberry (r= 0.604), blueberry/bilberry (r = 0.654), and black crowberry (r = 0.631). Participants also reported that berries appeared smaller (r = 0.660) and ripening occurred later (r = 0.500). A small portion of observations from eastern Sub and Low Arctic communities indicated earlier ripening times (axis 2: r = 0.402). Patterns towards decreased berry quantity and quality were primarily driven by participant responses from Nain. Participant responses from Nain and Kugluktuk indicated decreases in cranberry abundance (axis 1: r = 0.419). Alternatively, participants from Kangiqsualujjuaq noted that cloudberry abundance had increased (r = 0.579) and that these berries ripened earlier than in the past (axis 2: r = 0.470). Significant increases in blueberry abundance were attributed to participant responses from Pond Inlet (axis 1: r = -0.417).

The increase in abundance of tree seedlings and saplings along axis 1 (r = 0.567) is mainly due to responses from Nain and Kangiqsualujjuaq. Correlations with axis 2 indicate that primarily eastern communities have generally observed increased plant abundance (r = 0.638), yet this was infrequently noted in Umiujaq. Furthermore, participants from all communities have observed significant increases in shrub abundance (axis 2: r = 0.628). As one participant from Kangiqsujuaq explains, “Avaalaqiaq (*Betula glandulosa* Michx. [Arctic dwarf birch]) used to grow along the ground, now they are more upright growing like the uqaujaq (Salix sp. [willow])” – Alasie Koneak (unpublished). This pattern was largely influenced by responses from eastern

Sub/Mid Arctic communities. One Elder from Nain linked changes in berries to increased shrub expansion, explaining that “Those shrubs, avaalaKiak (Arctic dwarf birch), are affecting berries quite a bit because you know the berry leaves, they are being covered by those things. [...] less berries now maybe because of those avaalaKiak” – Verona Ittulak (unpublished). Relatively few participants from Pangnirtung and Baker Lake observed significant decreases in shrub abundance (axis 2: r = -0.427). Observations of vegetation change did not correlate strongly with 30-year trends in climate variables (Fig. 2.3b).

Animals

Many participants, irrespective of community, observed changes in animal populations (Fig. 2.3c). Along axis 1 (30.3% of VE), there were strong correlations driven by primarily eastern communities that mammal (r = 0.760), fish (r = 0.610) and bird (r = 0.586) abundance has changed. Participants from eastern communities described declines in seal and caribou abundance. From the High Arctic, one Elder explains that “There used to be seal swimming by Pond Inlet […] There is less seal every year now. Where are they going? There’s no more caribou herd anymore. Very few on Baffin” – Abraham Kunnuk (pg.129). These observations correlated with increased spring precipitation (axis 1: r = 0.471), especially for Pond Inlet, Nain and Kangiqsujuaq (Fig. 3). Correlations along axis 2 (30.1% of VE) depict strong similarity among all communities that insect abundance has changed (r = -0.833). A relatively small number of participants from all communities observed a decrease in mosquito abundance (r = -0.723), while participants from mainly Kugluktuk observed a decrease in black fly abundance (r= -0.448). Increases in the same species were observed along axis 3 (not shown), however agreement was very low within communities.

The age of participants did not correlate strongly with ordination axes and/or interview responses for any environmental variables considered (Table 2.6).

2.4 Discussion

Using ordination to combine Inuit TEK and climate trends helped to reveal multi-level patters (pan-Canadian Arctic, regional and local) in observed environmental change (Table 2.7), with some regional patterns (travel routes, rainfall, sea-ice conditions and animal abundance) correlating strongly with changing precipitation regimes. Results suggest that global, regional and local factors influence how impacts are observed within communities, supporting the need for locally informed climate change policy and adaptation strategies. This general finding is consistent with other new, mixed-method approaches to presenting and interpreting Inuit TEK on climate change (Cuerrier et al. 2015, Rapinski et al. 2017). Greater attention to local factors (ecological and social) alongside regional climate trends will be essential to identify patterns and drivers of observed change.

2.4.1 Climate trends, Inuit TEK, and patterns in their relationship across the Canadian Arctic

Two important findings emerged from our climate trend analyses. Firstly, the direction of trends was largely consistent among communities, suggesting that communities are similarly affected by large-scale climate patterns. Our results support general findings from other studies that Canada’s North, on average, has become warmer in recent decades, with some regions becoming wetter while others are experiencing less precipitation (Furgal and Prowse 2008; Bush and Lemmen 2019). Secondly, there was considerable variation in the magnitude of change for each community, indicating local controls on climate. This pattern was reflected in participant observations, and is well documented in the literature (Rapaić et al. 2015). Overall lack of significant trends across all climate variables may be partly explained by differences in rates of warming between western and eastern regions of northern Canada. While western Canada experienced rapid warming from 1970-1990’s, eastern Canada experienced a cooling trend (Morgan et al. 1993), warming only since the mid-1990’s (Finnis and Bell 2015). Weak trends may also be attributed to use of high-resolution gridded data, which rely on local stations to generate monthly means, but interpolates missing values (which are more frequent with historic data) from the nearest station. These results underscore the importance of continued local climate monitoring, as interpolated averages may not meaningfully relate to observed impacts at local scales (Rapaić et al. 2015). The distinct cooling trends we detected for Pangnirtung are consistent with climate trends reported in LeBlanc et al. (2010), although the authors also reported a recent warming trend from 1996-2009.

Inuit observations revealed Canadian Arctic-wide changes in primarily winter conditions, including the timing of seasons, decreased snowfall, later sea-ice freeze-up and earlier break-up, the latter of which correlated with increasing fall and annual precipitation. These patterns are consistent with Inuit TEK of change in snow and ice conditions reported from 12 communities across the Canadian Arctic (Nickels et al. 2005) and fit with the effects of climate warming on winter snow and ice regimes noted in remote sensing and modeling studies (ACIA 2005, Bhatt et al. 2010). Inuit observations that were similar in the east included altered travel routes, thinning sea-ice, and increased rainfall versus observations of decreased rainfall in western and central Canada; these local observations strongly correlated with fall and annual precipitation patterns for respective communities. Thus, precipitation appears to be an important local factor in driving large-scale patterns of observed change in weather and physical factors. We also identified a significant regional pattern among eastern communities (axis 1: r = -0.437; axis 2: r = 0.426) that “Way of life” is being affected by changes in the environment. Inuit identity and attachment to the land is essential to community mental health and well-being (Cunsolo Willox et al. 2012) and facilitates opportunities for transmission of TEK to youth (Cuerrier et al. 2012). Widespread effects on “Way of Life” point to the broader and intergenerational implications of climate change impacts across the Canadian Arctic.

Inuit TEK indicating pan-Canadian increases in shrub abundance, and an increase in plant abundance among eastern communities is an important and new contribution to tundra vegetation research (Sturm et al. 2001, Tape et al. 2006, Myers-Smith et al. 2011, Elmendorf et al. 2012). Inuit TEK from Nain and Kangiqsualujjaq was also consistent with dendrochronology studies that trees are more abundant now (Dufour-Tremblay et al. 2012, Lemus-Lauzon et al. 2012, Tremblay et al. 2012). General observations of vegetation change did not correlate strongly with climate trend variables (Table 2.6); however, they coincided with increasing annual and summer temperatures for nearly all communities (less in Pangnirtung). Higher temperatures result in higher degree day units, which among other factors such as winter snow cover, soil disturbances and herbivory, have all been linked to tree and shrub expansion in tundra ecosystems (Hallinger et al. 2010, Myers-Smith et al. 2011, Elmendorf et al. 2012). Other locally driven patterns include strong agreement among Nain residents that berry quantity and quality has declined. This local pattern was divergent from nearby Kangiqsualujjaq, which observed more cloudberries and earlier ripening times. Although significant relationships were not observed between Nain observations of declining berry crops and frost day frequency in the ordination, Nain stands out as the only community with an increase (albeit non-significant) in frost day frequency from 1977-2007. The timing and frequency of freeze-thaw events can directly influence the survival and productivity of tundra berry plants (Bokhorst et al. 2011), and could be an important local factor contributing to strong agreement among Nain residents. In general, fruit production was affected more by microclimate than macroclimate, and other local factors such as soil properties and the presence of sufficient pollinators (Shevtsova et al. 1995, Jacquemart and Thompson 1996, Krebs et al. 2009). Therefore, greater emphasis on the variation in local geography and microclimate could be used to explain and further explore observed changes in vegetation across communities.

Inuit have experienced pan-Canadian Arctic increases and decreases in abundance of northern insects, and this result contributes to a growing literature on the climate-driven changes in abundance and phenology of biting and pollinating insects (Olesen et al. 2008, Høye et al. 2013). There was strong similarity in observations among eastern communities (particularly Pond Inlet, Kangiqsujuaq and Nain) that mammal abundance has changed, which correlated with increasing spring precipitation. Because locally important fauna varied among communities, we were unable to make consistent species-specific comparisons across communities. However, participant narratives from eastern communities described declines in seal and caribou abundance. The association between mammal abundance and spring precipitation is potentially very important, since the timing and onset of spring are determining factors in migration and reproduction of Arctic fauna. For example, Stirling and Smith (2004) observed that early spring rainfall events compromise ringed seal survival on the coast of Baffin Island by melting subnivean layers necessary for thermoregulation and protection of seal pups. Sharma et al. (2009) predicted that continued increases in temperature and precipitation could alter caribou herd dynamics by shifting forage availability, and hence foraging behaviour, migration patterns, and demography. A more thorough species-specific approach to the interview questionnaire would be required to further explore trends in specific animal populations and climate variables across communities. Although participants described the change, they did not speculate or provide climate-based or otherwise explanations for the observed change in animal abundance. Widespread patterns were also observed for changes in bird and fish abundance; however, agreement within communities was low.

MRPP results indicated that gender may play a role in observations of weather/physical factors, yet high within-community variability in responses for this interview category made it difficult to detect clear patterns. Although it was outside the scope of this study, examining community-gender interactions and other socio-economic factors, such as employment, education, climate change awareness and land-use history may help clarify the variability observed for all ordinations, and better explain patterns of observed change across communities.

2.4.2 Ordination – benefits and risks

From a western scientific perspective, ordination was successful in presenting patterns in assemblages of Inuit observations across a broad geographic and culturally rich area that would otherwise be challenging to accomplish with traditional qualitative analysis approaches. Ordination created important visual tools and metrics for identifying patterns within the depth and spatial complexity of Inuit TEK, which can inform existing conservation and management systems (Cuerrier et al. 2015). While this result does not address the more fundamental issue that colonial systems still dominate global conservation and land management regimes (Dominguez and Luoma 2020), this analysis helps bring Inuit TEK to the forefront of decision makers for wider integration into existing policy, management and adaptation planning frameworks.

The patterns in Inuit observations described in this study closely align and build upon the consensus-based community summaries presented in Gerin-Lajoie et al. (2016). Whereas the qualitative approach presented in Gerin-Lajoie et al. (2016) can stand alone, this study relies on the narratives presented in Gerin-Lajoie et al. (2016) to provide context and deeper meaning to the observed patterns. This analytical approach could be further strengthened by including Inuit explanations for observed change and incorporating them into the analysis as environmental variables.

2.4.3 Conclusions

Overall, ordination was a useful analytical tool for aggregating Inuit TEK on multiple environmental variables with climate trend analyses over a broad geographic area. Inuit knowledge revealed national, regional and local-scale controls on how environmental change is experienced, and coupled with climate analyses, annual, fall and spring precipitation were identified as potential drivers of observed change. Inuit TEK brought to light new insights on changes in shrub, plant and insect abundance, and identified shrub expansion as a potential mechanism for declining berry quantity and quality in Nain.

Given the geographic scope of this study, and the extent of topics covered in the interviews, we were unable to expand our discussion with participants to seek out Inuit explanations for why certain changes are occurring, climate-driven or otherwise. This is an important next step for this research and would better extend the application of this study to climate change adaptation planning frameworks. The utility of ordination in collaborative and/or mixed methods research could be further realized by including local ecological and social factors to better account for variability within communities. Overall, this study highlights and supports the need for inclusion of local perspectives in climate change adaptation policy and adaptation response initiatives.

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Table 2.1 Locations and characteristics of the eight Canadian Arctic communities in this study.

Region Community	Latitude/ Longitude	Location	Vegetation Type[1]	Permafrost type[2]	Population[3]	Number of participants	Year(s) interviewed
Nunavut							
Kugluktuk	67.82 N 155.10 W	Western low Arctic	Tussock-sedge, dwarf-shrub, moss tundra	C	1450	17	2010
Baker Lake	67.31 N 96.02 W	Central low Arctic	Erect dwarf-shrub tundra	C	1872	24	2009
Pangnirtung	66.14 N 65.70 W	Eastern mid Arctic	Prostrate/hemiprostrate dwarf-shrub tundra	C	1425	19	2008/2009
Pond Inlet	72.70 N 77.96 W	Eastern high Arctic	Prostrate dwarf-shrub, herb tundra	C	1549	15	2008/2009
Nunavik							
Umiujaq	56.55 N 76.54 W	Eastern sub-arctic	Forest-tundra	D	445	20	2009
Kangiqsualujjuaq	58.71 N 65.99 W	Eastern sub-arctic	Forest-tundra	C/D	874	17	2007/2008
Kangiqsujuaq	61.59 N 71.95 W	Eastern low Arctic	Forest tundra, erect/dwarf-shrub tundra	C	696	9	2007/2008
Nunatsiavut							
Nain	56.54 N 61.69 W	Eastern sub-arctic	Forest-tundra	D	1188	23	2009/2010

[1] Vegetation type interpreted from Circumpolar Arctic Vegetation Map (CAVM Team 2003);
[2] C = continuous, D = discontinuous (CAVM Team 2003);
[3] Population estimates obtained from Statistics Canada Census 2011 (http://www12.statcan.gc.ca/census-recensement/index-eng.cfm)

Table 2.2 Theil-Sen slopes, Kendall's tau of 30-year (1977-2007) trends in climate variables, and 95% confidence intervals (respectively) calculated from monthly mean high-resolution gridded climate data (CRU TS3.11). Bold values indicate significance at p <0.05.

	Kugluktuk	Baker Lake	Pond Inlet	Pangnirtung	Umiujaq	Kangiqsujuaq	Kangiqsualujjuaq	Nain
Annual	**0.07; 0.366**	**0.08; 0.416**	**0.05; 0.315**	**-0.09; 0.310**	**0.07; 0.297**	0.05; 0.246	0.04; 0.209	0.01; 0.113
TMP*	**(0.03, 0.11)**	**(0.02, 0.13)**	**(0.0, 0.09)**	**(-0.15, -0.03)**	**(0.01, 0.12)**	(-0.02,0.11)	(0.01, 0.09)	(-0.03, 0.07)
Spring	0.07; 0.232	**0.06; 0.301**	0.05; 0.191	**-0.13; -0.269**	0.06; 0.103	0.05; 0.177	0.03; 0.085	-0.01; -0.021
TMP	(-0.02, 0.15)	**(-0.01, 0.15)**	(-0.03, 0.12)	**(-0.24, -0.01)**	(-0.04,0.14)	(-0.03, 0.12)	(-0.04, 0.1)	(-0.07, 0.07)
Summer	**0.05; 0.352**	**0.06; 0.398**	0.03; 0.209	**-0.08; -0.320**	**0.07; 0.480**	0.03; 0.168	0.02; 0.186	0.01; 0.076
TMP	**(0.01, 0.10)**	**(0.03, 0.11)**	(-0.01,0.05)	**(-0.15, -0.01)**	**(0.03, 0.11)**	(-0.01, 0.06)	(0.00, 0.04)	(-0.01,0.04)
Fall	0.08; 0.209	**0.09; 0.306**	**0.10; 0.283**	-0.07; -0.159	**0.08; 0.508**	**0.07; 0.320**	**0.06; 0.347**	**0.04; 0.260**
TMP	(-0.01, 0.20)	**(-0.02, 0.19)**	**(0.0, 0.18)**	(-0.13, 0.02)	**(0.03, 0.14)**	**(-0.02, 0.14)**	**(0.00, 0.12)**	**(-0.02, 0.09)**
Winter	0.09; 0.218	**0.07; 0.264**	0.00; 0.062	-0.04; -0.090	0.06; 0.255	0.04; 0.182	0.04; 0.177	0.02; 0.099
TMP	(0.00, 0.17)	**(-0.02, 0.15)**	(-0.07,0.11)	(-0.13, 0.02)	(0.0, 0.15)	(-0.06, 0.14)	(-0.07,0.14)	(-0.08, 0.11)
Annual	-1.50; -0.255	-0.58; -0.060	1.73; 0.143	**-3.62; -0.306**	1.16; 0.149	-0.54; 0.025	**4.79; 0.356**	3.20; 0.237
PRE*	(-3.51, 0.08)	(-2.91, 0.7)	(-0.49, 3.47)	**(-8.54, -1.13)**	(-1.10, 3.41)	(-3.58,1.65)	**(2.85, 6.81)**	(0.99, 5.45)
Spring	-0.45; -0.103	-0.16; -0.088	0.14; 0.134	-0.46; -0.228	-0.12; -0.094	-0.30; -0.113	0.20; 0.048	0.20; 0.117
PRE	(-1.30, 0.20)	(-0.69, 0.11)	(-0.11, 0.58)	(-1.30, 0.03)	(-0.72, 0.60)	(-0.99, 0.38)	(-0.62,0.9)	(-0.67,1.07)
Summer	0.60; 0.009	0.00; -0.018	0.63; 0.125	**-2.83; -0.375**	-0.73; -0.090	0.06; -0.016	**3.76; 0.411**	**2.07; 0.264**
PRE	(-1.63, 2.08)	(-1.39, 1.85)	(-0.33, 1.63)	**(-5.48, -0.44)**	(-2.65, 0.97)	(-1.69, 1.84)	**(1.91, 5.42)**	**(1.09, 3.27)**
Fall	-0.30; -0.157	-0.25; -0.102	0.19; 0.123	-0.77; -0.048	0.04; 0.080	-0.16; 0.011	0.25; 0.080	0.31; 0.062
PRE	(-0.83, 0.10)	(-1.2, 0.25)	(-0.39, 0.92)	(-2.54, 0.59)	(-0.66, 0.70)	(-0.95, 0.51)	(-0.72,1.12)	(-0.58,1.24)
Winter	-0.58; -0.126	-0.03; 0.046	**0.55; 0.258**	0.14; 0.099	**1.28; 0.324**	0.08; 0.094	0.63; 0.159	-0.02; 0.044
PRE	(-1.25, 0.07)	(-0.46, 0.41)	**(-0.1, 1.13)**	(-0.52, 0.74)	**(0.05, 2.71)**	(-0.76, 1.4)	(-0.73, 2.18)	(-1.96, 2.62)
Annual	**-0.70; -0.494**	-0.08; -0.053	0.05; 0.125	**-1.36; -0.536**	0.06; 0.034	**-0.48; -0.315**	0.02; 0.030	0.12; 0.011
WDF*	**(-0.92, -0.46)**	(-0.23, 0.08)	(-0.04, 0.12)	**(-1.76, -0.97)**	(-0.30, 0.42)	**(-0.76, -0.17)**	(-0.27, 0.33)	(-0.22, 0.45)
Annual	**-0.22; -0.297**	**-0.28; -0.321**	-0.07; -0.110	0.00; 0.097	**-0.47; -0.465**	**-0.28; -0.377**	-0.14; -0.161	0.03; 0.080
FDF*	**(-0.52, 0.00)**	**(-0.44, -0.08)**	(-0.24, 0.11)	(0.00, 0.00)	**(-0.72, -0.22)**	**(-0.42, -0.11)**	(-0.33, 0.0)	(-0.20, 0.23)

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[1] CRU TS3.1 – Climatic Research Unit Time Series 3.1, University of East Anglia CRU, 2011 (http://badc.nerc.ac.uk/browse/badc/cru/data/cru_ts/cru_ts_3.10/data); TMP = temperature; PRE = precipitation; WDF = wet day frequency; FDF = frost day frequency

Table 2.3 Multi-response permutation procedure (MRPP) statistics for comparison of participant responses among communities and between men and women for eight Canadian Arctic communities. Bold values indicate significance at p <0.05*.

	Community			Gender		
	T	A	*p*	T	A	*p*
Weather/Physical Factors	-28.405	0.107	**0.000**	-2.777	0.004	**0.015**
Vegetation/Berries	-31.245	0.149	**0.000**	0.379	-0.001	0.576
Animals	-13.730	0.101	**0.000**	0.116	0.000	0.453

***** T=Test statistic; A = Chance-corrected within-group agreement [1- (observed delta/expected delta)]; *p* = probability of smaller or equal delta.

Table 2.4 Multi-response permutation procedure (MRPP) statistics for pairwise comparisons of participant responses between communities. Bold values indicate significance at *p* <0.05*. Pairwise community comparisons are ordered from west to east for eight Canadian Arctic communities.

			Weather/Physical Factors			Vegetation/Berries			Animals		
Pairwise Community Comparisons			T	A	*p*	T	A	*p*	T	A	*p*
Kugluktuk	vs.	Baker Lake	-11.871	0.068	**0.000**	- 4.715	0.033	**0.001**	- 6.537	0.075	**0.000**
Kugluktuk	vs.	Pond Inlet	-12.379	0.097	**0.000**	- 7.033	0.062	**0.000**	- 6.716	0.087	**0.000**
Kugluktuk	vs.	Pangnirtung	-11.460	0.079	**0.000**	- 5.353	0.048	**0.000**	- 8.505	0.121	**0.000**
Kugluktuk	vs.	Umiujaq	-12.391	0.086	**0.000**	- 8.493	0.074	**0.000**	- 5.461	0.069	**0.001**
Kugluktuk	vs.	Kangiqsujuaq	-14.816	0.101	**0.000**	- 5.012	0.035	**0.000**	- 6.713	0.073	**0.000**
Kugluktuk	vs.	Kangiqsualujjuaq	-10.135	0.097	**0.000**	- 8.709	0.092	**0.000**	- 0.829	0.014	0.173
Kugluktuk	vs.	Nain	-16.542	0.111	**0.000**	-17.047	0.152	**0.000**	- 9.427	0.096	**0.000**
Baker Lake	vs.	Pond Inlet	- 9.400	0.050	**0.000**	- 4.496	0.029	**0.001**	- 8.432	0.092	**0.000**
Baker Lake	vs.	Pangnirtung	- 9.633	0.046	**0.000**	- 3.093	0.023	**0.011**	- 2.414	0.032	**0.033**
Baker Lake	vs.	Umiujaq	- 7.760	0.038	**0.000**	-10.201	0.076	**0.000**	- 1.205	0.014	0.111
Baker Lake	vs.	Kangiqsujuaq	-14.459	0.075	**0.000**	- 6.665	0.038	**0.000**	- 7.070	0.072	**0.000**
Baker Lake	vs.	Kangiqsualujjuaq	-10.330	0.066	**0.000**	-10.776	0.084	**0.000**	- 3.123	0.043	**0.013**
Baker Lake	vs.	Nain	-20.092	0.117	**0.000**	-19.073	0.135	**0.000**	-11.989	0.108	**0.000**
Pond Inlet	vs.	Pangnirtung	0.068	0.000	0.448	- 4.661	0.042	**0.001**	- 5.070	0.066	**0.001**
Pond Inlet	vs.	Umiujaq	- 1.812	0.012	0.057	-11.358	0.110	**0.000**	- 5.399	0.061	**0.001**
Pond Inlet	vs.	Kangiqsujuaq	- 4.447	0.026	**0.001**	- 3.846	0.026	**0.003**	- 0.405	0.004	0.291
Pond Inlet	vs.	Kangiqsualujjuaq	- 1.731	0.015	0.060	- 7.439	0.077	**0.000**	0.482	-0.007	0.635
Pond Inlet	vs.	Nain	- 9.885	0.070	**0.000**	-18.390	0.165	**0.000**	- 1.163	0.012	0.124
Pangnirtung	vs.	Umiujaq	- 3.188	0.018	**0.009**	- 4.818	0.047	**0.002**	0.387	-0.005	0.557
Pangnirtung	vs.	Kangiqsujuaq	- 9.809	0.053	**0.000**	- 4.340	0.032	**0.003**	- 6.860	0.085	**0.000**
Pangnirtung	vs.	Kangiqsualujjuaq	- 2.635	0.018	**0.016**	- 8.676	0.098	**0.000**	- 3.020	0.049	**0.015**
Pangnirtung	vs.	Nain	-15.302	0.100	**0.000**	-18.440	0.167	**0.000**	-11.049	0.119	**0.000**

Umiujaq	vs.	Kangiqsujuaq	-10.606	0.061	**0.000**	- 9.725	0.070	**0.000**	- 5.918	0.063	**0.000**
Umiujaq	vs.	Kangiqsualujjuaq	- 6.391	0.048	**0.000**	-12.363	0.155	**0.000**	- 2.034	0.029	**0.046**
Umiujaq	vs.	Nain	-14.484	0.093	**0.000**	-21.093	0.212	**0.000**	-10.531	0.102	**0.000**
Kangiqsujuaq	vs.	Kangiqsualujjuaq	- 3.683	0.024	**0.002**	- 4.177	0.030	**0.001**	0.064	-0.001	0.462
Kangiqsujuaq	vs.	Nain	- 7.441	0.041	**0.000**	-15.993	0.116	**0.000**	- 2.126	0.018	**0.035**
Kangiqsualujjuaq	vs.	Nain	- 8.472	0.067	**0.000**	-10.910	0.103	**0.000**	- 1.163	0.014	0.124

*****T=Test statistic; A = Chance-corrected within-group agreement (1- (observed delta/expected delta)); *p* = probability of smaller or equal delta.

Table 2.5 Pearson correlation coefficients (r-values)[1] of environmental change variables with ordination axes from three separate ordinations on interview responses in three general categories: Weather/Physical factors, Vegetation/Berries and Animals for eight Canadian Arctic communities*.

Weather/Physical factors			Vegetation/Berries			Animals		
	Axis 1	Axis 2		Axis 1	Axis 2		Axis 1	Axis 2
Winter[2]	**-0.658**	-0.137	Plants more	0.300	**0.638**	Insects	0.322	**-0.833**
Spring[2]	**-0.470**	-0.088	Plants less	0.048	-0.299	Mammals	**0.760**	0.228
Summer[2]	**-0.577**	-0.286	Bloom later	0.233	-0.026	Birds	**0.586**	0.033
Fall[2]	**-0.514**	-0.341	Bloom earlier	-0.353	0.364	Fish	**0.610**	0.255
Weather (variability)	-0.379	0.070	Trees more	**0.567**	**0.431**	Black flies more	-0.078	-0.396
Wind	**-0.409**	0.125	Trees less	0.191	-0.003	Black flies less	0.233	**-0.448**
Snowmelt	0.086	0.161	Shrubs more	0.303	**0.628**	Black flies later	0.088	-0.207
Hydrology	-0.197	-0.085	Shrubs less	0.013	**-0.427**	Black flies sooner	-0.151	0.240
Permafrost	-0.38	-0.27	Grass more	-0.203	0.260	Mosquitoes more	-0.020	-0.094
Erosion	-0.369	-0.147	Grass less	0.023	-0.168	Mosquitoes less	0.374	**-0.723**
Travel routes	**-0.538**	**0.523**	Lichens more	0.237	0.068	Mosquitoes later	0.227	0.017
Way of life	**-0.437**	**0.426**	Lichens less	0.215	-0.072	Mosquitoes sooner	-0.258	0.074
Sunlight	-0.006	0.319	Berries more	-0.291	0.000			
Temp. warmer	0.019	0.213	Berries less	**0.800**	-0.048			
Temp. colder	**-0.487**	0.128	Ripen later	**0.500**	0.006			
Rain more	-0.317	**0.469**	Ripen earlier	0.135	**0.402**			
Rain less	-0.082	**-0.578**	Berry taste	NA	NA			
Snow more	0.175	-0.006	Berries bigger	-0.390	0.248			
Snow less	**-0.563**	-0.095	Berries smaller	**0.660**	-0.165			
Sea-ice freeze-up later	**-0.522**	0.064	Cloudberry[3] more	-0.202	**0.579**			
Sea-ice freeze-up earlier	0.039	-0.268	Cloudberry less	**0.604**	0.018			
Sea-ice break-up later	0.000	-0.398	Cloudberry later	-0.075	-0.045			

Sea-ice break-up earlier	-0.282	**0.662**	Cloudberry earlier	-0.055	**0.470**
Sea-ice thicker	-0.092	-0.117	Blueberry[3] more	**-0.417**	0.047
Sea-ice thinner	-0.341	**0.636**	Blueberry less	**0.654**	0.134
Lake-ice freeze-up later	-0.337	0.154	Blueberry later	-0.051	0.129
Lake-ice break-up later	0.007	0.001	Blueberry earlier	-0.309	0.066
Lake-ice break-up earlier	-0.221	0.217	Crowberry[3] more	-0.366	0.033
Lake-ice thicker	-0.128	0.158	Crowberry less	**0.631**	0.051
Lake-ice thinner	-0.392	**0.423**	Crowberry later	-0.004	0.236
			Crowberry earlier	-0.250	0.039
			Cranberry[3] more	-0.127	0.324
			Cranberry less	**0.419**	-0.113
			Cranberry later	0.104	-0.141
			Cranberry earlier	-0.003	0.134

---

[1] Interview responses with r-values ≥ |0.400| were considered statistically significant and therefore plotted in Fig. 2.3 (see text for details)

[2] Refers to changes observed in timing and duration of seasons

[3] Cloudberry = *Rubus chamaemorus* L.; Blueberry = *Vaccinium uliginosum* L.; Crowberry = *Empetrum nigrum* L.; Cranberry = *V. vitis-idaea* L.

* All ordinations resulted in a 3-dimensional solution, however only the first two dimensions were retained. Final stress and instability values for each ordination were: a) Weather/Physical factors = 18.93; <0.0001, b) Vegetation/Berries = 13.07; <0.0001, and c) Animals = 13.34; <0.0001

Table 2.6 Pearson correlation coefficients (r-values)[1] of climate trends and age of participant with NMDS ordination axes from three separate ordinations on interview responses in three general categories: Weather/Physical factors, Vegetation/Berries and Animals for eight Canadian Arctic communities.

	Weather/Physical factors		Vegetation/Berries		Animals	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Age	0.191	-0.016	0.025	-0.062	0.027	-0.060
Annual TMP*	-0.058	-0.170	-0.131	-0.149	-0.013	-0.205
Spring TMP	-0.016	-0.178	-0.219	-0.198	-0.035	-0.215
Summer TMP	0.019	-0.241	-0.101	-0.147	-0.150	-0.198
Fall TMP	-0.072	0.090	-0.014	0.090	0.047	-0.084
Winter TMP	-0.045	-0.200	-0.029	-0.076	-0.158	-0.250
Annual PRE*	-0.191	**0.449**	0.212	0.369	0.346	0.107
Spring PRE	-0.320	0.279	0.275	0.191	**0.471**	0.072
Summer PRE	-0.372	0.270	0.273	0.314	**0.437**	-0.035
Fall PRE	-0.014	**0.528**	0.014	0.326	0.325	0.277
Winter PRE	0.349	0.287	-0.269	0.095	-0.062	0.256
Annual WDF*	-0.024	0.216	0.140	0.092	0.157	0.075
Annual FDF*	-0.187	0.159	0.370	0.126	0.267	0.158

[1] Climate variables with r-values ≥ |0.400| were considered statistically significant and therefore plotted in Fig. 2 (see text for details); TMP = temperature; PRE = precipitation; WDF = wet day frequency; FDF = frost day frequency

Table 2.7 Summary of geographic patterns in environmental change based on interpretation of NMDS ordination of Inuit knowledge and climate variables across eight Canadian Arctic communities. Presentation of variables follows that of Table 2.5.

		Geographic extent of observed change*		
Interview category	Observations	Pan-Canadian Arctic	Regional	Local
Weather/ physical factors	Timing of seasons	All		
	Wind	All		
	Travel routes		Eastern Sub/Low, High Arctic	
	Way of Life		Eastern	
	Temperature colder			Nain
	Rain more		Eastern	
	Rain less		Western/central	
	Snow less	All		
	Sea-ice freeze-up later	Coastal		
	Sea-ice break-up earlier	Coastal		
	Sea-ice thinner		Eastern Sub/Low, High Arctic	
	Lake-ice thinner			Nain, Kangiqsujuaq
Vegetation/ berries	Plants more		Eastern	
	Trees more			Nain; Kangiqsualujjuaq
	Shrubs more	All		
	Shrubs less			Pangnirtung↓, Baker Lake↓
	Berries less			Nain
	Ripen later			Nain
	Ripen earlier		Eastern Sub/Low↓	
	Berries smaller			Nain
	Cloudberry more			Kangiqsualujjuaq
	Cloudberry less			Nain
	Cloudberry earlier			Kangiqsualujjuaq
	Blueberry more			Pond Inlet
	Blueberry less			Nain

	Crowberry less			Nain
	Cranberry less			Nain↓, Kugluktuk↓
Animals	Insect abundance	All		
	Mammal abundance		Eastern	
	Bird abundance		Eastern	
	Fish abundance		Eastern	
	Black flies less			Kugluktuk
	Mosquitoes less	All↓		

*All = all communities; Coastal = All communities but Baker Lake; Western/Central Arctic = Kugluktuk and Baker Lake; Eastern = All but Kugluktuk and Baker Lake; High Arctic = Pond Inlet; Mid Arctic = Pangnirtung; Eastern Sub-Arctic = Umiujaq, Kangisualujjuaq, Nain; Eastern Low Arctic = Kangiqsuajuaq; ↓ indicates significant variables driven by few participant observations; Cloudberry = *Rubus chamaemorus* L.; Crowberry = *Empetrum nigrum* L.; Blueberry = *Vaccinium uliginosum* L. (blueberry); Cranberry = *V. vitis-idaea* L.

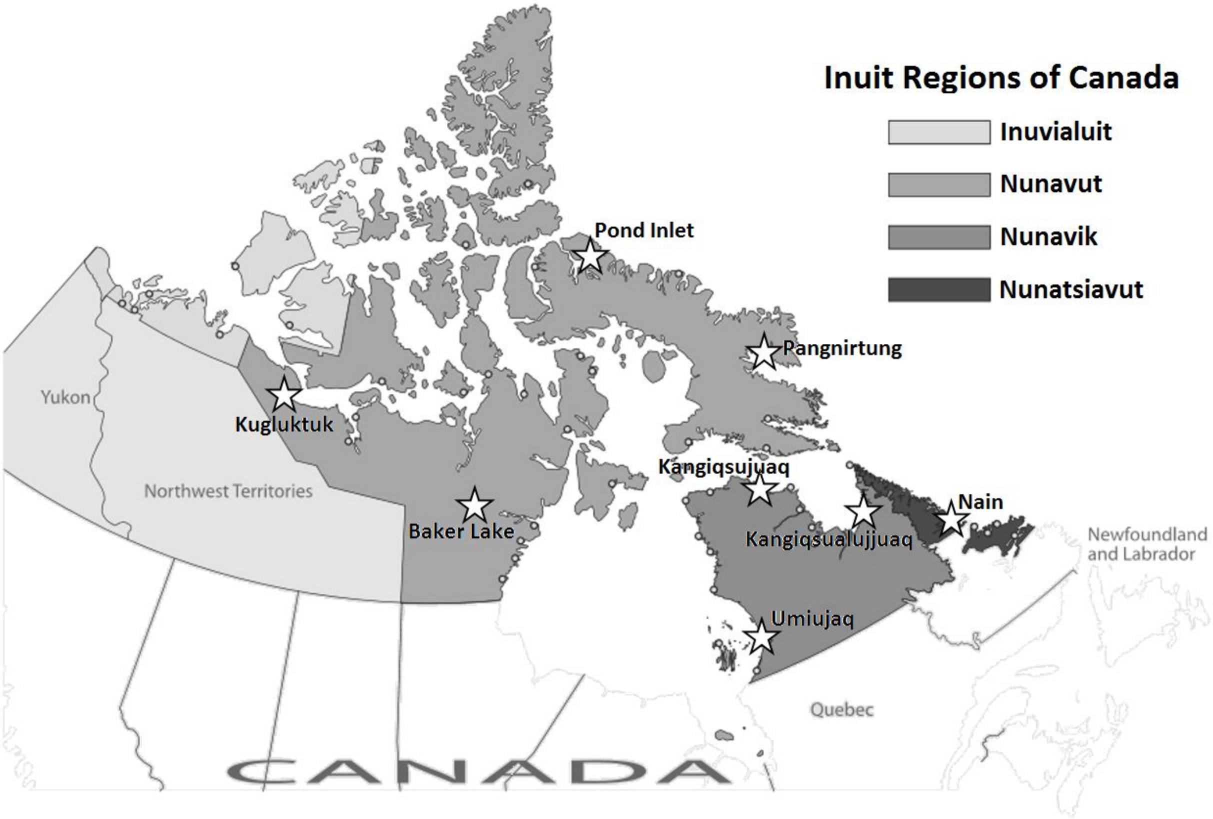


Fig. 2.1 Map of Canada highlighting the locations of participating communities across the Inuit regions of Canada. White stars indicate participating communities. White dots indicate all other Inuit communities within each region (Modified from: Maps of Inuit Nunangat (Inuit Regions of Canada), 2008, Inuit Tapiriit Kanatami; https://www.itk.ca/publication/maps-inuit-nunangat-inuit-regions-canada).

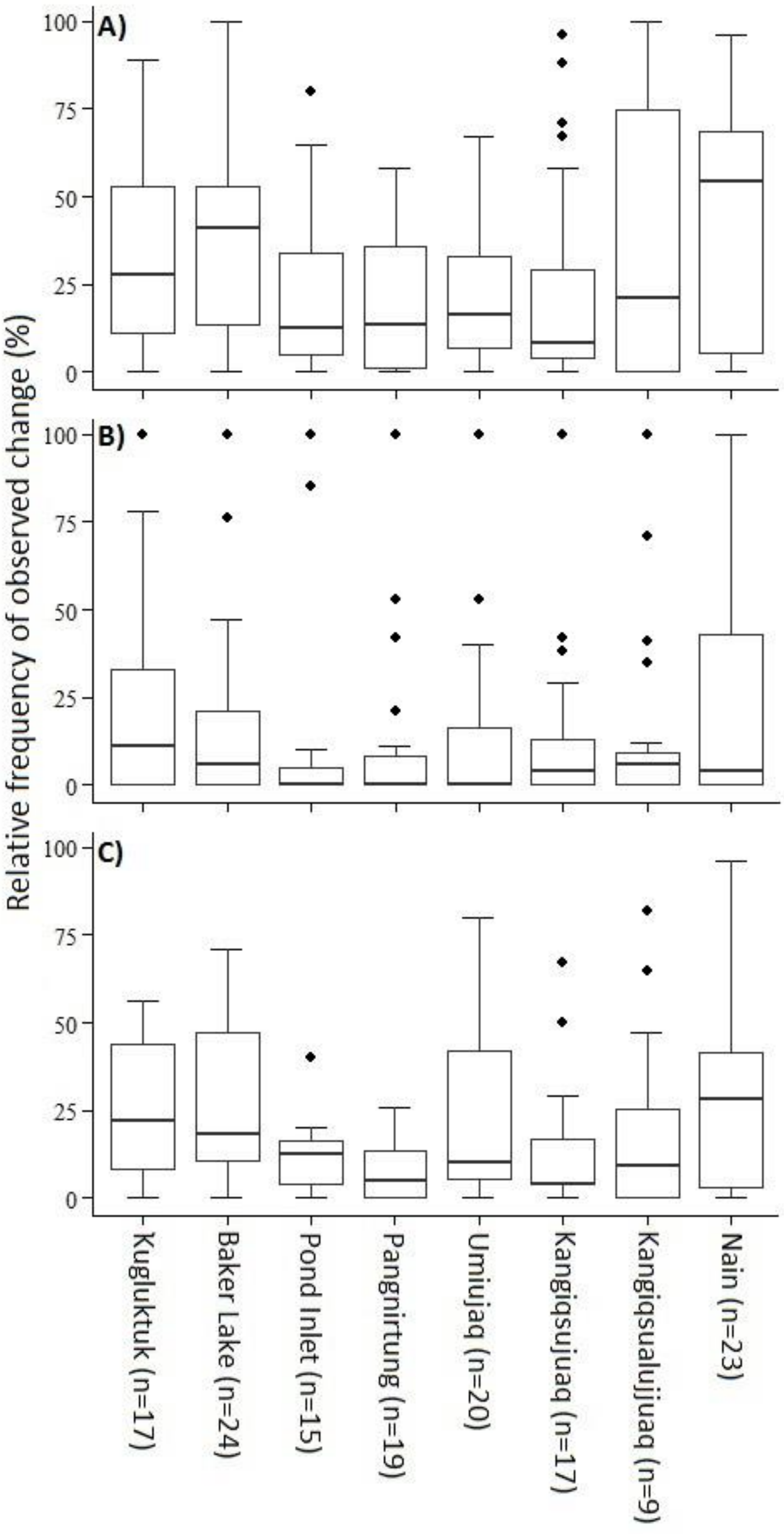
A)
B)
C)
Relative frequency of observed change (%)
0
25
50
75
100
Kugluktuk (n=17)
Baker Lake (n=24)
Pond Inlet (n=15)
Pangnirtung (n=19)
Umiujaq (n=20)
Kangiqsujuaq (n=17)
Kangiqsualujjuaq (n=9)
Nain (n=23)

Fig. 2.2 Boxplots showing the distribution of values (median, interquartile range, min/max and outliers) for the relative frequency of observed change (%) within A) Weather/physical factors B) Vegetation/berries and C) Animals across communities. Communities are ordered from west to east. Comparatively short boxes indicate a high level of consistency of observed change vs. long boxes which indicate greater variability in observed change within individual communities.

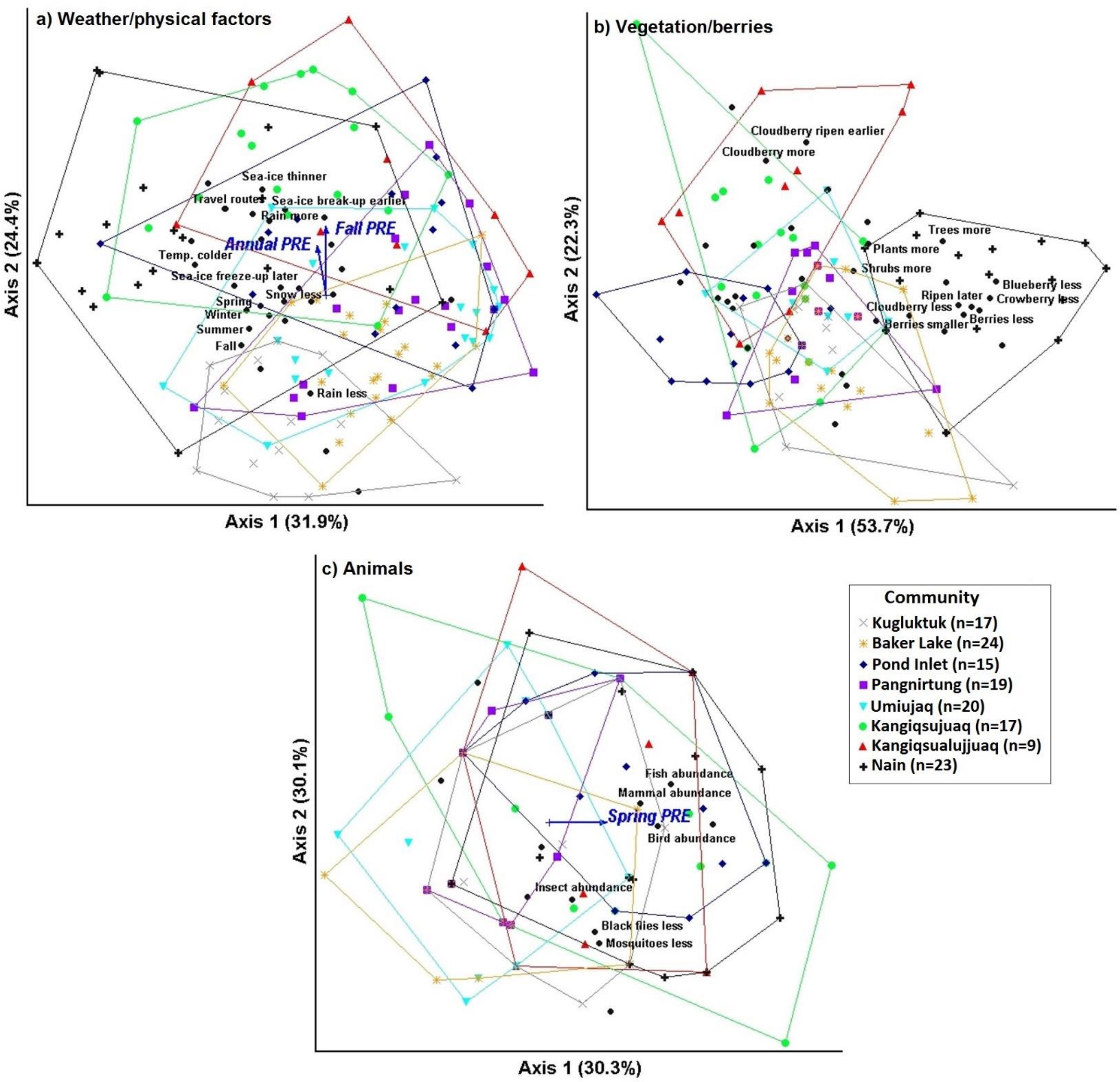
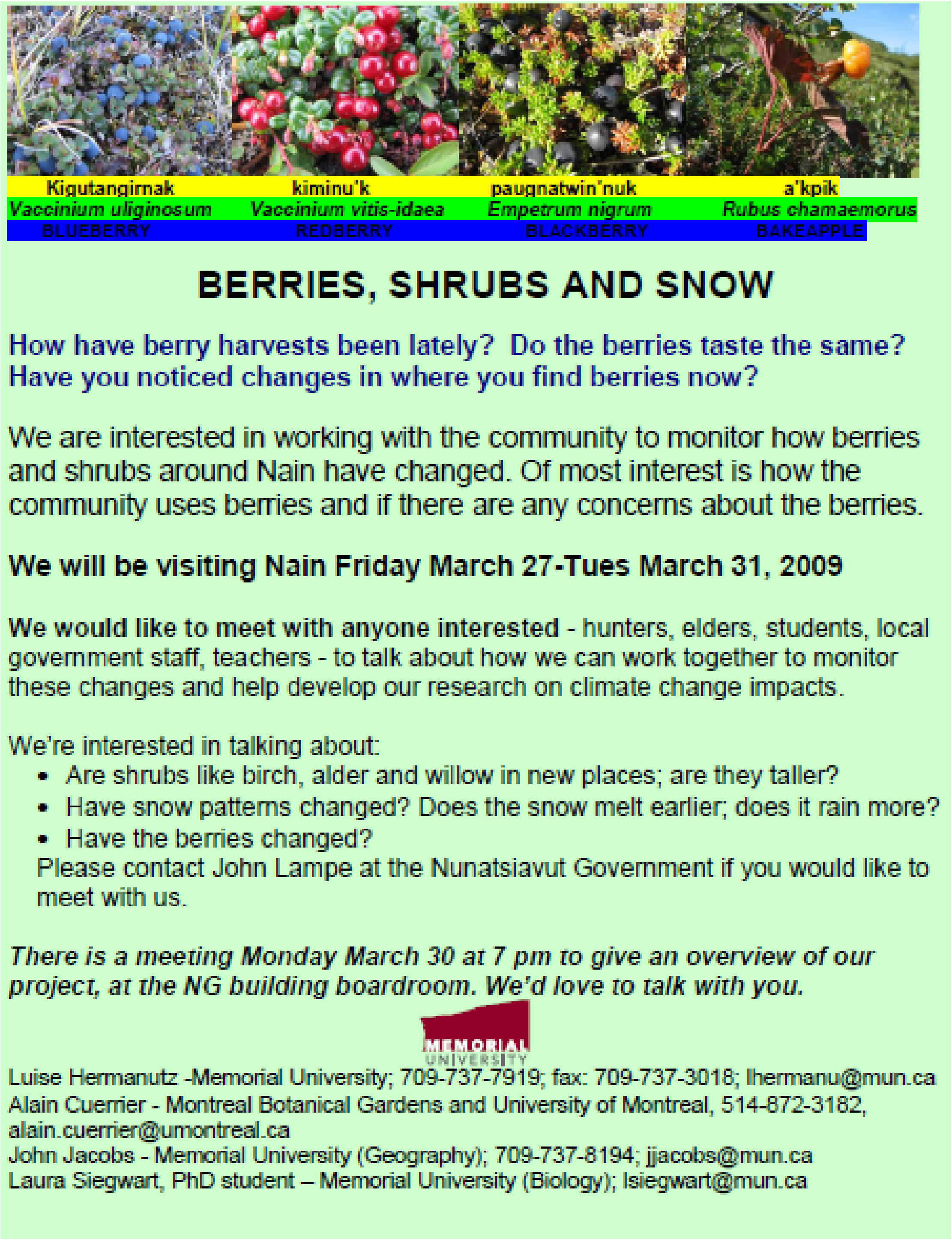


Fig. 2.3 Ordination diagram (NMS with Euclidean distance) showing separation of responses regarding a) Weather/physical factors, b) Vegetation/berries and c) Animals from 144 interview participants, within and among eight Canadian Arctic communities. Responses for each community are shown by unique symbols, colours and convex

hulls, which enclose points from a community. Environmental variables are shown with labels as closed black circles. Blue vectors represent interview response correlations with climate time series over a 30-year period (1977-2007). The direction and length of climate vectors indicate strength of the correlation. PRE = precipitation.

Appendix 2.1 Sample poster used for Snowball Sampling in Nain, Nunatsiavut, April 2009.



Kigutangirnak	kiminu'k	paugnatwin'nuk	a'kpik
Vaccinium uliginosum	*Vaccinium vitis-idaea*	*Empetrum nigrum*	*Rubus chamaemorus*
BLUEBERRY	REDBERRY	BLACKBERRY	BAKEAPPLE

BERRIES, SHRUBS AND SNOW

How have berry harvests been lately? Do the berries taste the same? Have you noticed changes in where you find berries now?

We are interested in working with the community to monitor how berries and shrubs around Nain have changed. Of most interest is how the community uses berries and if there are any concerns about the berries.

We will be visiting Nain Friday March 27-Tues March 31, 2009

We would like to meet with anyone interested - hunters, elders, students, local government staff, teachers - to talk about how we can work together to monitor these changes and help develop our research on climate change impacts.

We're interested in talking about:

- Are shrubs like birch, alder and willow in new places; are they taller?
- Have snow patterns changed? Does the snow melt earlier; does it rain more?
- Have the berries changed?

Please contact John Lampe at the Nunatsiavut Government if you would like to meet with us.

There is a meeting Monday March 30 at 7 pm to give an overview of our project, at the NG building boardroom. We'd love to talk with you.

MEMORIAL UNIVERSITY

Luise Hermanutz -Memorial University; 709-737-7919; fax: 709-737-3018; lhermanu@mun.ca
Alain Cuerrier - Montreal Botanical Gardens and University of Montreal, 514-872-3182, alain.cuerrier@umontreal.ca
John Jacobs - Memorial University (Geography); 709-737-8194; jjacobs@mun.ca
Laura Siegwart, PhD student – Memorial University (Biology); lsiegwart@mun.ca

Appendix 2.2 Interview questionnaire used throughout this study.

Date of interview:	Name of interviewee/elder:
Place of interview:	Date of birth:
Name of interpreter:	Place of birth:
Name of interviewer:	Heritage (Cultural Group):
Start Time:	CODE:
End Time:	

Consent form signature: ☐ Payment Claim Form Attached: ☐

NOTE: Before the interview, make sure participant knows that there is no right or wrong answer for any of the questions. Any knowledge that they share with us is helpful and valuable for both scientific and cultural reference. All interviews will be documented and archived for consultation and future generations to learn from.

A. QUESTIONS ABOUT BERRIES:

1. Do you go berry picking?
2. What berries do you pick? Do you have a favourite berry? Why?
3. Do you have local names for these berries? For stages of ripening?
4. How do you pick the berries? The same or different techniques?
5. Who do you pick berries with? Was it always this way?
    a. Do you have rules when berry picking?
6. How do you choose your berry picking spots?
    a. Do you go to the same spots every year or rotate?
    b. Do you use patterns in the landscape (hills, bogs, fields, dry, wet)?
    c. The presence of other plant species that grow with particular berry plants?
7. What leads to a good berry crop?
8. What leads to a poor berry crop?
9. Have you detected differences in the recent past in timing of when berry plants:
    a. Flower? Visited by insects?
    b. Set fruit? Ripening?
    c. Other differences in look, taste, quality of berries?

10. Are the conditions different now from when you picked berries in the past (e.g. bug nets)?
11. Where do you go berry picking for (indicate it on the map? – will remain confidential):
    a. Aqpiq/Arpiq/Okpik/ **A'kpiq** (*Rubus chamaemorus*)
    b. Paurngaq/Paurngaq/XX/ **Paugnatwi'nuk** (*Empetrum nigrum*)
    c. Kegotangenak/Kigutangirnaq/ XX/**XX** (*Vaccinium uliginosum*)
    d. Kimminaq/ Kimminaq/ XX/Kimimino'k, **kiminu'k** (*Vaccinium vitis-idaea*)
    e. Kallaq/XX/XX/**XX** (*Arctostaphylos alpina*)
12. Are there places you used to go berry picking where you no longer go?
    a. Why?
    b. Where are these places located?

Note: Ask how the participant is doing (if he/she is still interested in answering questions). If not, we can take a break, or come back at another time, or terminate the interview here.

B. QUESTIONS ABOUT CHANGE AND BERRIES

1. Have you/not seen changes in the vegetation throughout your life?
    a. New plants not seen before? If so, can you describe and/or name them?
    b. Plants becoming more common? Or less common? Rare?
    c. Plants becoming taller? Bigger?
2. Have you noticed changes in the distribution and abundance of:
    a. Trees?
    b. Shrubs?
    c. Berry producing plants?
    d. Lichens
3. If so, why do you think these changes are occurring?
4. Have these changes influenced your way of:
    a. Hunting?
    b. Fishing?
    c. Traveling on the tundra?
5. Have you seen any changes in the emergence, distribution or number of:
    a. Miluqiaq (black flies)?
    b. Kitturiaq (mosquitoes)?
    c. Igutsak (bumblebees)?
    d. Saralikitaq (butterflies)?
6. Do you know if animals (caribou, geese, ptarmigan, lemming, mice etc.) eat:
    a. Berries
    b. Shrubs
    c. Lichens

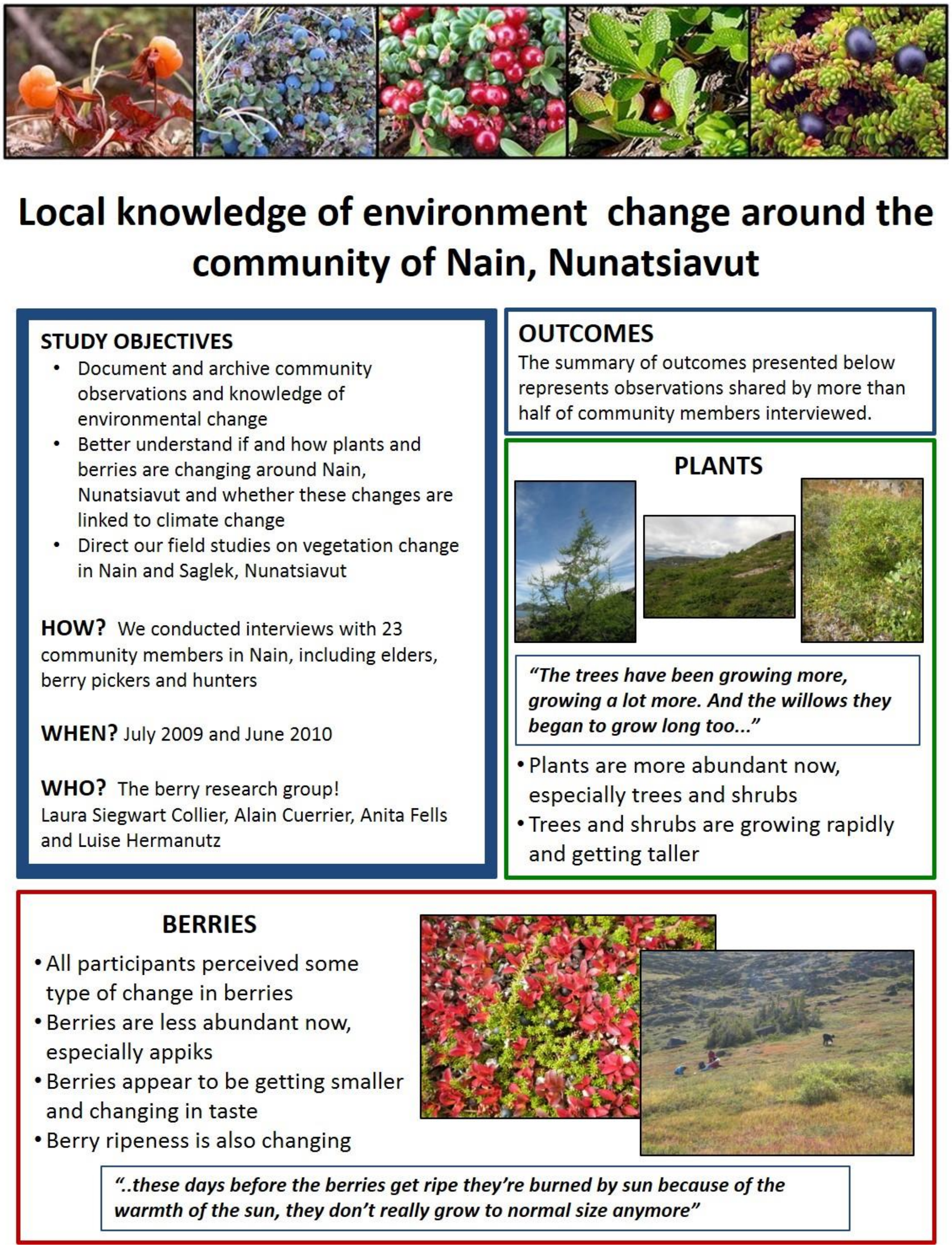
7. Have you ever seen animals eating berries? Found berries in the stomachs of animals (bears, birds, caribou)?
8. Have you observed landscape modifications (disturbance, erosion, avalanche)?
    a. If so, where?
    b. Do you/not have an explanation?
9. Have you seen changes in snow cover? In snow quality?
    a. If so, can you explain it?
    b. Did it affect plants?
    c. Did it affect humans and animals?
10. Have you/not seen any changes concerning lakes (tasiq) and rivers (kuutjuaq)?
11. Have you/not seen any changes concerning rain (surujuk)?
12. Have you/not seen any changes concerning wind (anuri)?
13. Have you/not seen any changes concerning permafrost (frozen ground) and active layer (e.g.: softer ground)?

Note: Ask how the participant is doing (if he/she is still interested in answering questions). If not, we can take a break, or come back at another time, or terminate the interview here.

C. TRADITIONAL USE OF BERRIES

1. How do you use the berries you have collected? Do you preserve them? How?
2. How did your mother and grandmother preserve their berries?
3. Do you have any concerns about the future of berry producing plants?
4. Are you/not concerned with possible changes affecting:
    a. Shrub abundance?
    b. Distribution of berry producing plants?
    c. Yield of berry producing plants?
    d. The taste of the berries?
    e. Their juiciness?
    f. Insects in berries?
5. Is there something else you would like to talk about?

Appendix 2.3 Sample summary report used to share within-community results to participants in Nain, Nunatsiavut.



Local knowledge of environment change around the community of Nain, Nunatsiavut

STUDY OBJECTIVES

- Document and archive community observations and knowledge of environmental change
- Better understand if and how plants and berries are changing around Nain, Nunatsiavut and whether these changes are linked to climate change
- Direct our field studies on vegetation change in Nain and Saglek, Nunatsiavut

HOW? We conducted interviews with 23 community members in Nain, including elders, berry pickers and hunters

WHEN? July 2009 and June 2010

WHO? The berry research group!
Laura Siegwart Collier, Alain Cuerrier, Anita Fells and Luise Hermanutz

OUTCOMES

The summary of outcomes presented below represents observations shared by more than half of community members interviewed.

PLANTS

> ***"The trees have been growing more, growing a lot more. And the willows they began to grow long too..."***

- Plants are more abundant now, especially trees and shrubs
- Trees and shrubs are growing rapidly and getting taller

BERRIES

- All participants perceived some type of change in berries
- Berries are less abundant now, especially appiks
- Berries appear to be getting smaller and changing in taste
- Berry ripeness is also changing

> ***"..these days before the berries get ripe they're burned by sun because of the warmth of the sun, they don't really grow to normal size anymore"***

SEA AND LAND ANIMALS



- Community members have observed a decrease in the abundance and quality of caribou and seal
- Black bears are seen more frequently around Nain, and polar bears are travelling closer to town

> *"like the seal, it (caribou) does not have that much fat anymore ... even the bone marrow is like watery"*

New animals seen around Nain: Moose and different species of songbirds!

WEATHER AND SEASONS

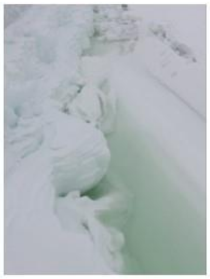

- The weather is more variable now and harder to predict
- The timing of seasons has changed, especially for winter
- The temperature is colder (in spring and summer)
- The strength and direction of winds have changed

Changes in the environment are affecting traditional way of life such as hunting, fishing and travelling on the land.

Special thanks to:

- All elders, hunters and berry pickers that participated in our consultations
- The community of Nain for welcoming our research team
- The Nunatsiavut Government – especially Wilson Jararuse for translation and interpretation
- Parks Canada Agency for logistic support

SNOW, ICE & RAIN



- There is less snow and more rain

- Sea ice freezes up later and breaks up earlier than in the past
- Sea ice is thinner now
- Lake/river ice is also changing

For more information, please contact:

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MEMORIAL UNIVERSITY

ArcticNet
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Institut de recherche en biologie végétale IRBV
JARDIN BOTANIQUE DE MONTRÉAL
Université de Montréal

Appendix 2.4 Pearson correlation coefficients between climate variables derived from high-resolution gridded (CRU-TS3.1[1]) and local climate station data (Environment Canada[2]) for time periods of local station data availability. Bold values indicate significance at $p < 0.05$.

Site	Kugluktuk	Baker Lake	Pond Inlet	Pangnirtung	Umiujaq	Kangiqsujuaq	Kangiqsualujjuaq	Nain
Data availability	1978-2007	1977-2007	1977-2007	1995-2007	1993-2007	1993-2007	1993-2007	1985-2007
Annual TMP*	**0.969**	**0.980**	**0.567**	-0.160	**0.964**	**0.664**	**0.864**	**0.858**
Spring TMP	**0.995**	**0.942**	**0.941**	0.402	**0.960**	**0.630**	**0.796**	**0.837**
Summer TMP	**0.970**	**0.974**	**0.460**	-0.073	**0.943**	0.130	**0.545**	**0.427**
Fall TMP	**0.980**	**0.970**	**0.874**	**0.732**	**0.942**	**0.758**	**0.830**	**0.869**
Winter TMP	**0.958**	**0.982**	**0.969**	0.307	**0.957**	**0.874**	**0.954**	**0.939**
Annual PRE*	**0.868**	**0.832**	0.262	-0.550	NLD*	NLD	NLD	**0.491**
Spring PRE	**0.986**	**0.723**	0.451	0.492	NLD	NLD	NLD	**0.674**
Summer PRE	**0.850**	**0.914**	0.308	-0.450	NLD	NLD	NLD	0.315
Fall PRE	**0.992**	**0.808**	0.392	0.241	NLD	NLD	NLD	**0.692**
Winter PRE	**0.967**	**0.858**	**0.490**	0.093	NLD	NLD	NLD	**0.498**

[1] CRU TS3.1 – Climatic Research Unit Time Series 3.1, University of East Anglia CRU, 2011 (http://badc.nerc.ac.uk/browse/badc/cru/data/cru_ts/cru_ts_3.10/data)

[2] Environment Canada Historical Climate Data (http://climate.weather.gc.ca/index_e.html; Accessed September, 2012)

* TMP = temperature; PRE = precipitation; NLD = no local data

Appendix 2.5 R code for trend analyses performed in R v 2.15.3 using the ‘zyp’ package (Bronaugh and Werner 2013).

```
>zyp.trend.vector
(Site$Variable,method=c("yuepilon"),conf.intervals=TRUE,preserve.range.for.sig.test=TRUE)
```

Site = communities listed in Table 2.1.

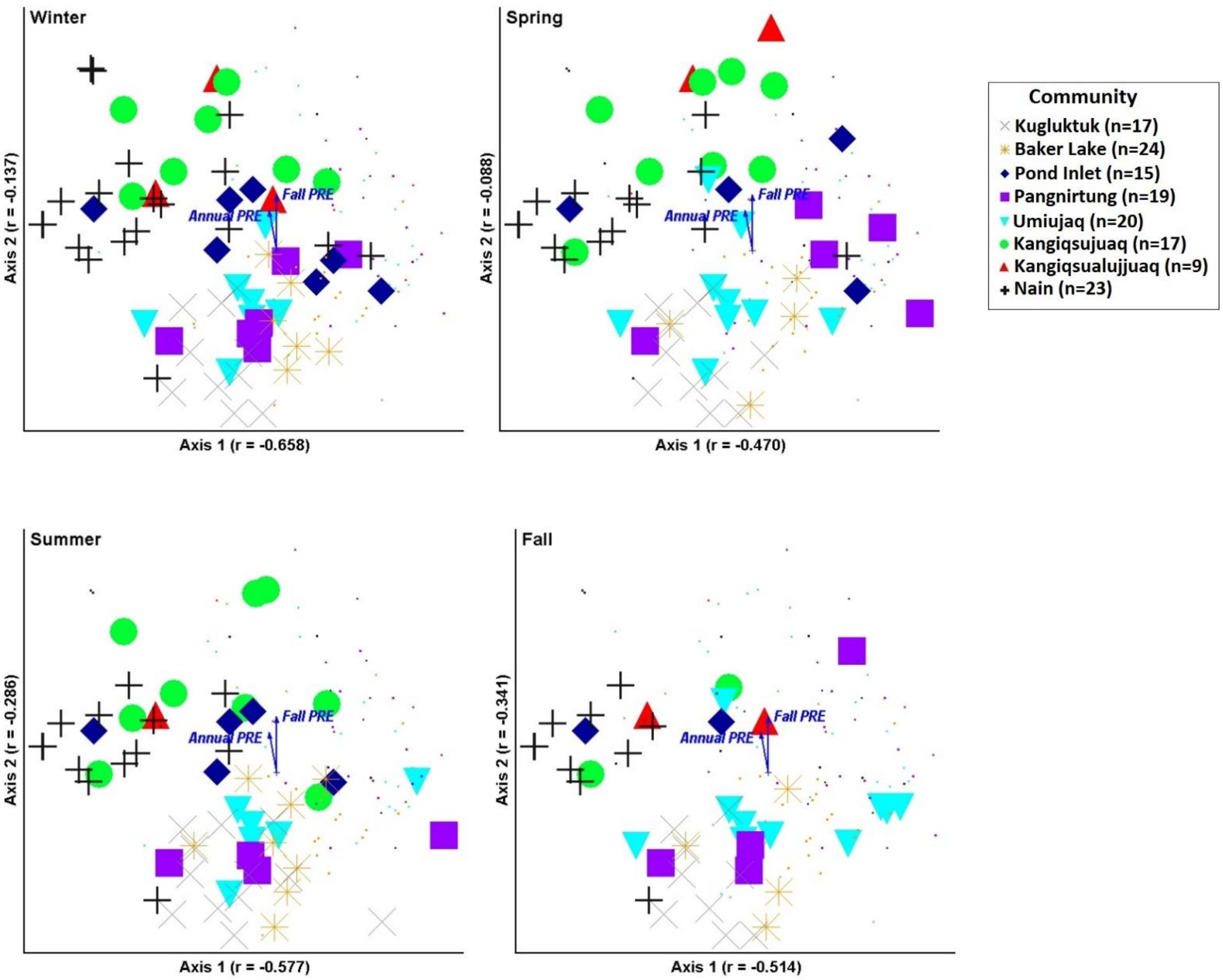
Variable = climate trend variables listed in Table 2.2.

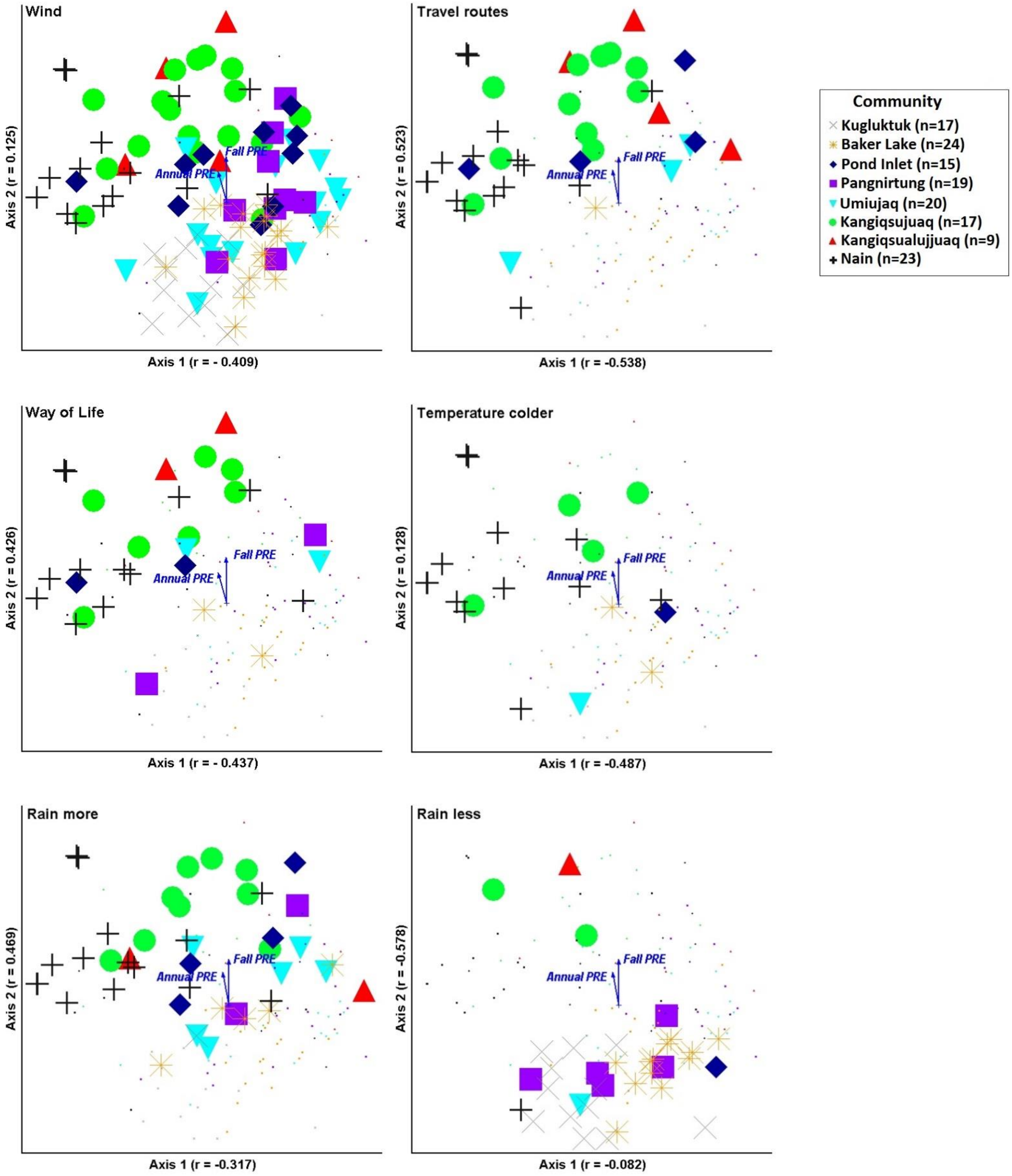
Appendix 2.6 Ordination plots representing scatterplots of first and second axes ordination scores for individual environmental variables that met the critical cut-off value of r = |0.450| (as presented in text and summarized in Table 2.5).

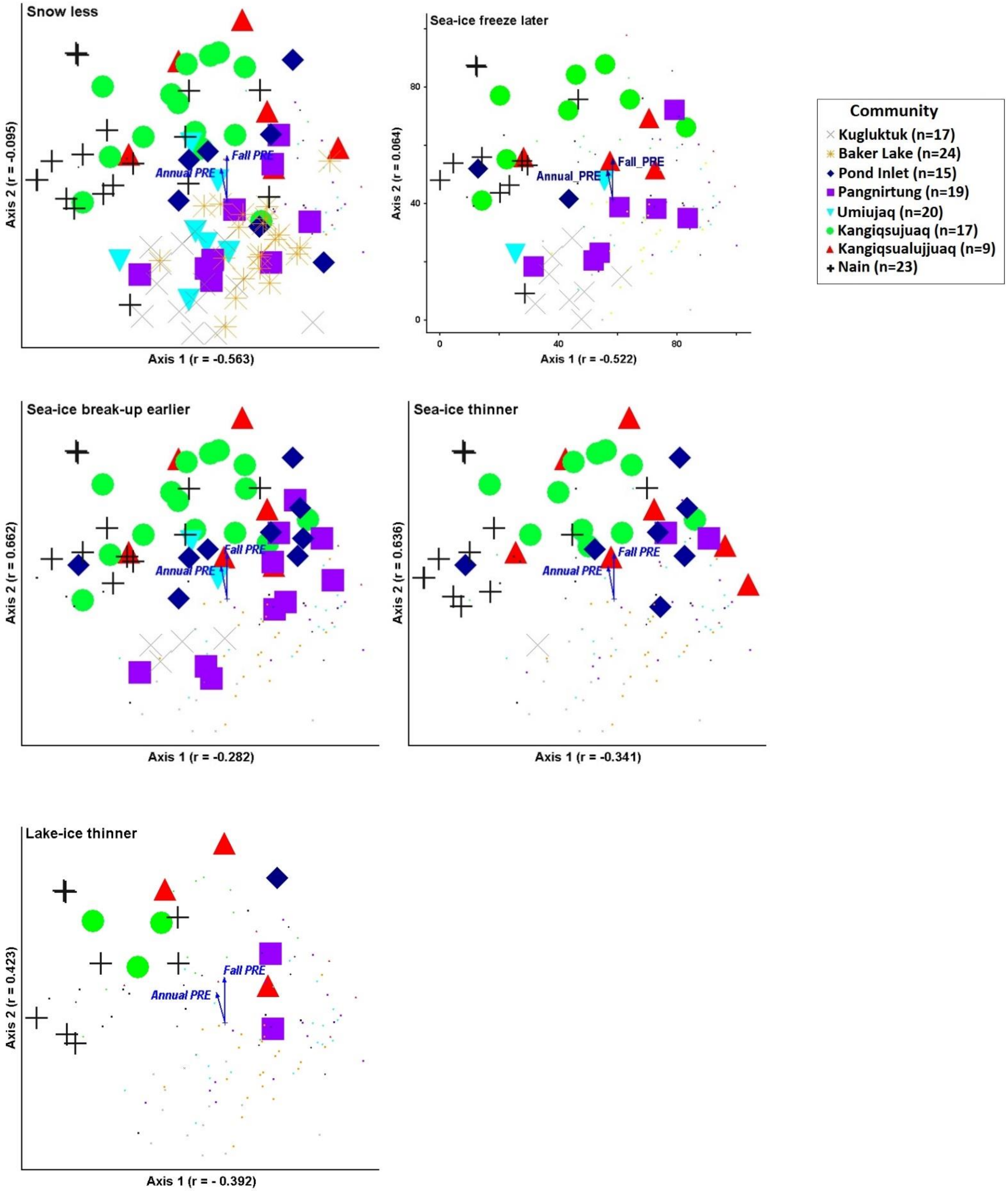
Notes on interpretation:

For each ordination scatterplot, the size of the sample units directly reflects the participants' response, such that large icons indicate a "1" for observed change, and small icons indicate a "0" for no change. The response variable presented is indicated in the upper left corner of each plot, and the r-values corresponding to Table 2.5 are provided in parentheses for each axis. These plots enabled us to look at patterns in interview responses across communities individually and support our interpretation of patterns in Fig. 2.3 (a-c).

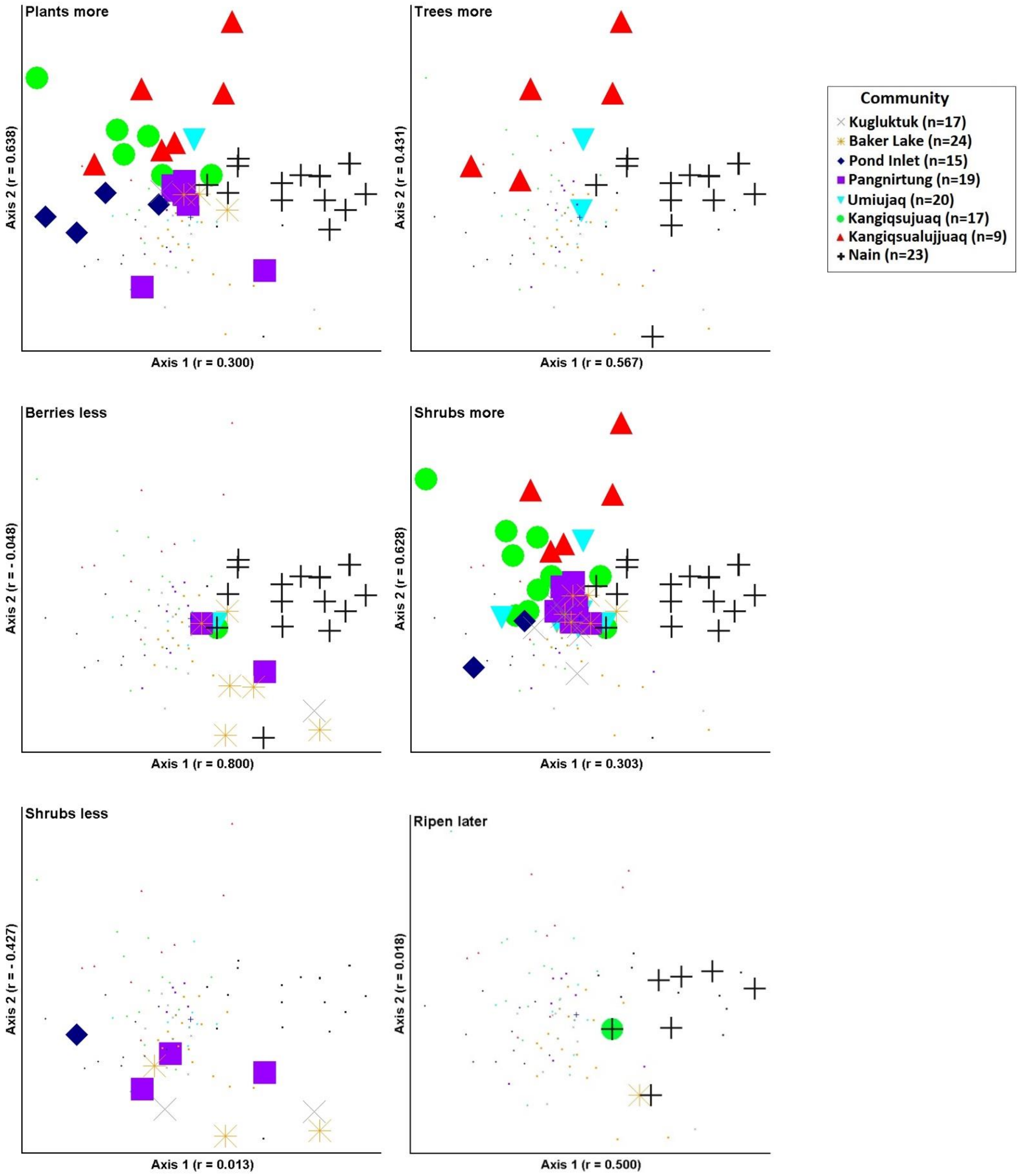
Individual scatterplots for Fig. 2.3a – Weather/physical factors

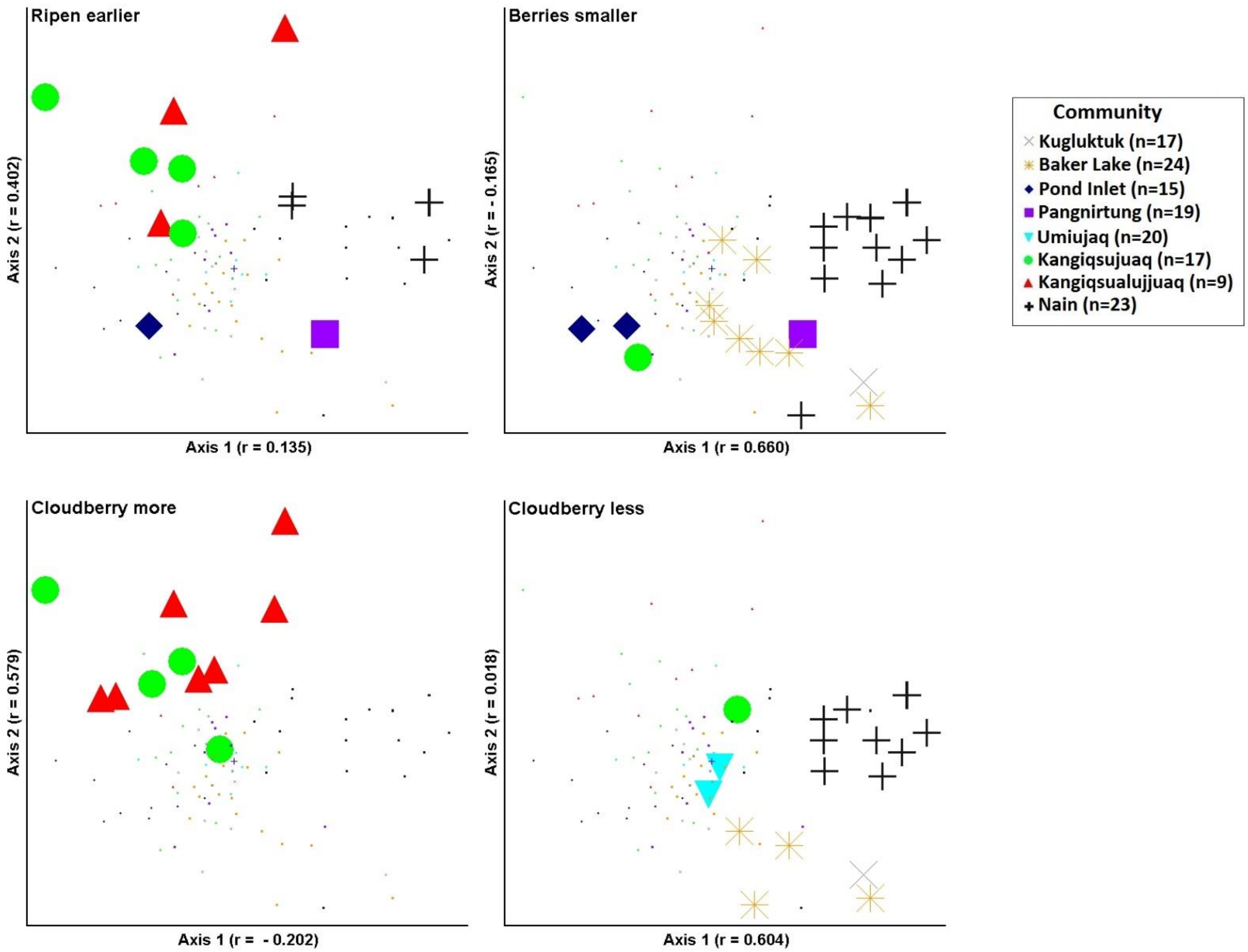


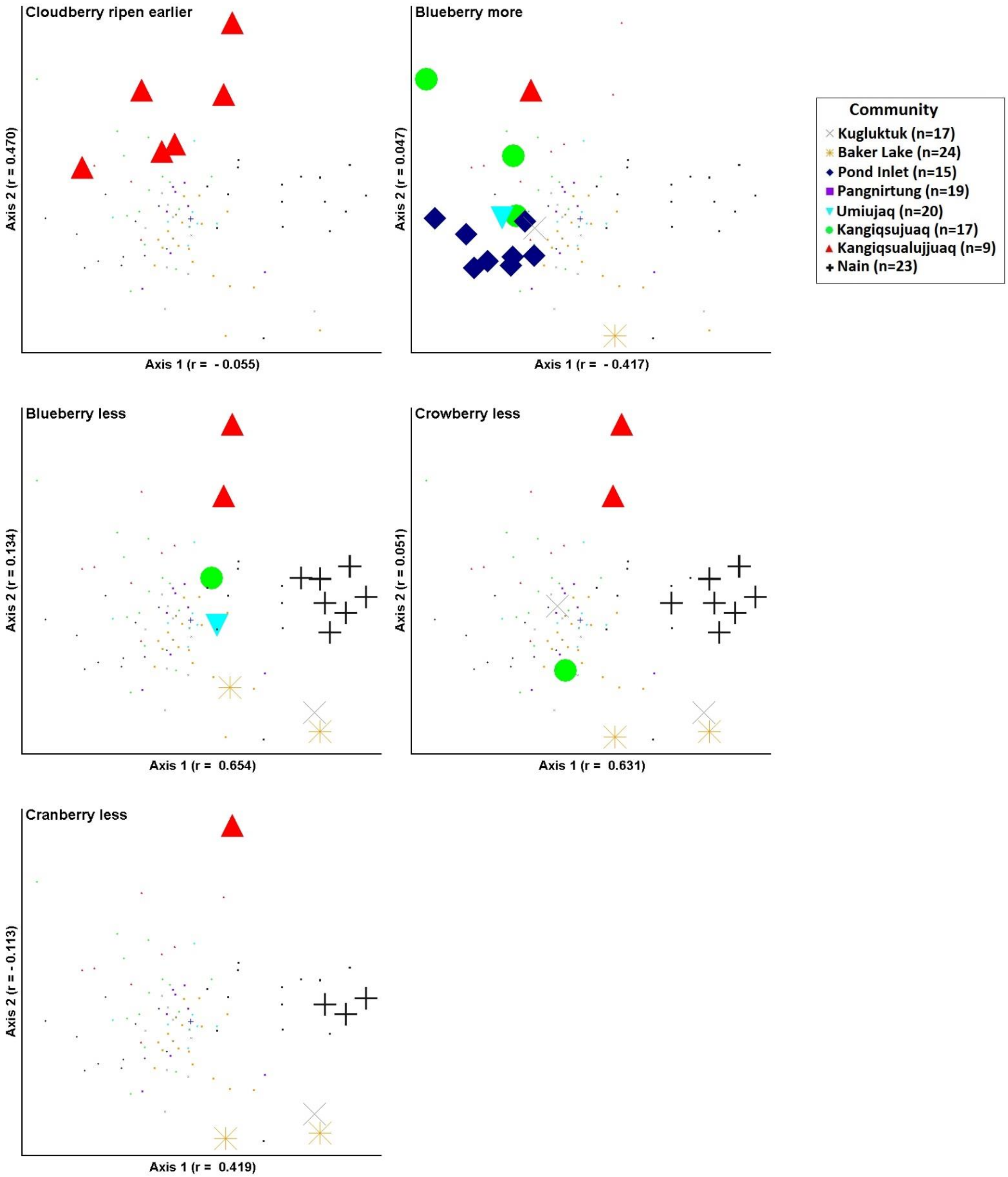

Wind
Axis 2 (r = 0.125)
Axis 1 (r = - 0.409)
Travel routes
Axis 2 (r = 0.523)
Axis 1 (r = -0.538)
Way of Life
Axis 2 (r = 0.426)
Axis 1 (r = - 0.437)
Temperature colder
Axis 2 (r = 0.128)
Axis 1 (r = -0.487)
Rain more
Axis 2 (r = 0.469)
Axis 1 (r = -0.317)
Rain less
Axis 2 (r = -0.578)
Axis 1 (r = -0.082)
Fall PRE
Annual PRE
Community
× Kugluktuk (n=17)
✳ Baker Lake (n=24)
◆ Pond Inlet (n=15)
■ Pangnirtung (n=19)
▼ Umiujaq (n=20)
● Kangiqsujuaq (n=17)
▲ Kangiqsualujjuaq (n=9)
+ Nain (n=23)


Snow less
Axis 2 (r = -0.095)
Axis 1 (r = -0.563)
Fall PRE
Annual PRE
Sea-ice freeze later
Axis 2 (r = 0.064)
Axis 1 (r = -0.522)
80
40
0
0
40
80
Fall_PRE
Annual_PRE
Community
× Kugluktuk (n=17)
✳ Baker Lake (n=24)
◆ Pond Inlet (n=15)
■ Pangnirtung (n=19)
▼ Umiujaq (n=20)
● Kangiqsujuaq (n=17)
▲ Kangiqsualujjuaq (n=9)
+ Nain (n=23)
Sea-ice break-up earlier
Axis 2 (r = 0.662)
Axis 1 (r = -0.282)
Fall PRE
Annual PRE
Sea-ice thinner
Axis 2 (r = 0.636)
Axis 1 (r = -0.341)
Fall PRE
Annual PRE
Lake-ice thinner
Axis 2 (r = 0.423)
Axis 1 (r = - 0.392)
Fall PRE
Annual PRE

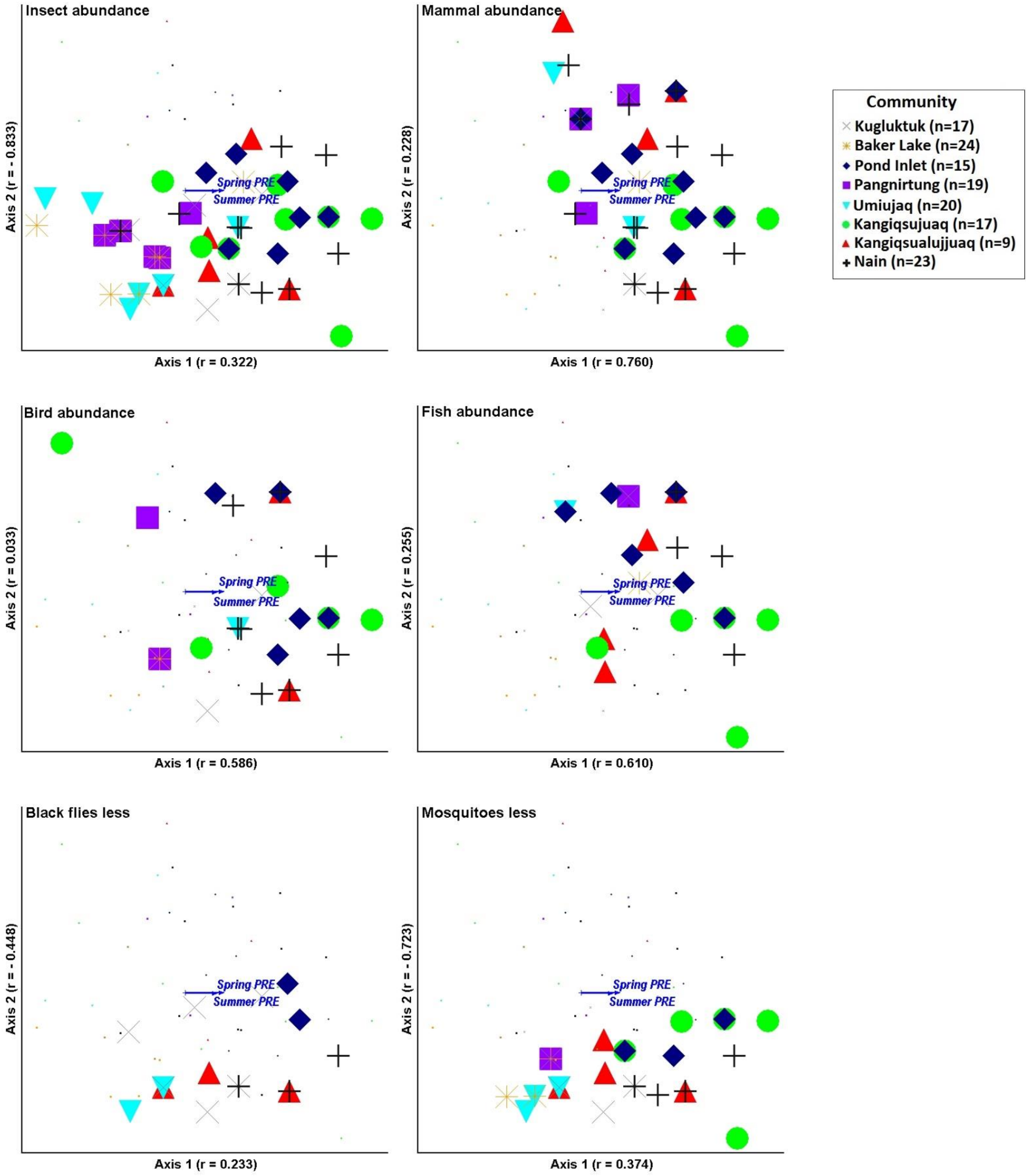
Individual scatterplots for Fig. 2.3b – Vegetation/berries




Ripen earlier
Axis 2 (r = 0.402)
Axis 1 (r = 0.135)
Berries smaller
Axis 2 (r = - 0.165)
Axis 1 (r = 0.660)
Cloudberry more
Axis 2 (r = 0.579)
Axis 1 (r = - 0.202)
Cloudberry less
Axis 2 (r = 0.018)
Axis 1 (r = 0.604)
Community
Kugluktuk (n=17)
Baker Lake (n=24)
Pond Inlet (n=15)
Pangnirtung (n=19)
Umiujaq (n=20)
Kangiqsujuaq (n=17)
Kangiqsualujjuaq (n=9)
Nain (n=23)


Cloudberry ripen earlier
Axis 2 (r = 0.470)
Axis 1 (r = - 0.055)
Blueberry more
Axis 2 (r = 0.047)
Axis 1 (r = - 0.417)
Community
× Kugluktuk (n=17)
✳ Baker Lake (n=24)
◆ Pond Inlet (n=15)
■ Pangnirtung (n=19)
▼ Umiujaq (n=20)
● Kangiqsujuaq (n=17)
▲ Kangiqsualujjuaq (n=9)
+ Nain (n=23)
Blueberry less
Axis 2 (r = 0.134)
Axis 1 (r = 0.654)
Crowberry less
Axis 2 (r = 0.051)
Axis 1 (r = 0.631)
Cranberry less
Axis 2 (r = - 0.113)
Axis 1 (r = 0.419)

Individual scatterplots for Fig. 2.3c – Animals



Chapter 3: Strong canopy-understory feedbacks on fruit production at treeline

Siegwart Collier, L. and L. Hermanutz.

Abstract

Evidence from multiple syntheses has shown that foundation species such as trees and tall shrubs are responding positively to warming climate throughout the tundra biome, yet the response is spatially heterogeneous. Whilst the advancement of these canopy formers into tundra ecosystems are predicted to change the structure and dynamics of lower stature plant communities, there is no consensus on community-level impacts. Canopy formation could have significant impacts on the performance (growth and fruit production) of dwarf berry shrubs, which are globally ubiquitous at treeline and throughout low-shrub tundra ecosystems. Many northern berry shrubs are culturally significant, and their berries serve as an essential summer and winter food source for northern peoples and wildlife. We anticipate that climate-induced changes to canopy structure will initiate a height-fruit production trade-off by increasing light competition between short, low-growing berry shrubs and their tall, upright neighbours. However, we predict that responses will vary, such that berry plants with truly prostrate growth forms will exhibit the greatest declines in fruit production, whereas those that can compete vertically for available light will be less affected. In this study, we investigate factors affecting the fruit production of three culturally important dwarf berry shrubs with varying capacities for upright growth (*Vaccinium vitis-idaea* < *Empetrum nigrum* <*V. uliginosum*) near Nain (Nunatsiavut, Labrador). We evaluated berry shrub performance across the forest-tundra ecotone by measuring performance traits (abundance, height and fruit

production) in relation to canopy and understory characteristics of the broader plant community at four elevational zones (forest, lower forest-tundra transition, upper forest-tundra transition, and low shrub tundra). Using a combination of ordination and hurdle models, we found that berry shrub performance differentiated most strongly among species at the interface between the lower and upper forest-tundra transition zone, where boreal and tundra communities diverge, corresponding to an increase in available light and other aboveground resources. Although we did not observe growth-reproduction trade-offs among species, characteristics of a closed canopy forest had consistent negative effects on the extent of fruit production for all berry species. Positive growth-reproduction relationships were exhibited for both *Vaccinium* species, indicating the importance of plant abundance in reproduction allocation among these species. The relative importance of abiotic versus biotic factors did not relate to prostrate vs. upright growth forms; however, we determined that different factors are important in explaining the presence vs. extent of fruit production for all species. This distinction could not have been made without the application of hurdle models. By documenting strong canopy-understory feedbacks on fruit production at treeline, this study substantiates the prediction that expansion of tree and tall-shrub canopy could reduce fruit production and thus availability of fruit throughout low shrub tundra ecosystems.

3.1 Introduction

Decades of research from an array of forest ecosystems demonstrate that canopy-forming species directly and indirectly influence understory vegetation dynamics through modification of light, soil moisture and resource availability (Riegel et al. 1992, Barbier et al. 2008, Halpern and Lutz 2013). At the forest-tundra ecotone (or treeline), where climatic factors have historically constrained species´ range limits (Smith et al. 2009), it is expected that climate warming will increase and extend canopy formation through upslope and northward advance of trees into tundra and tall shrubs into low-shrub tundra ecosystems (Callaghan et al. 2002, Myers-Smith et al. 2011). Whether treelines and shrublines advance (Hofgaard et al. 2009) or retreat (Harsch et al. 2009), global tundra greening and shifting canopy boundaries will have measurable impacts on understory plant community dynamics (Wookey et al. 2009, Pajunen et al. 2011). An increasing number of studies are exploring the potential for canopy formation (i.e. via shrubification) to either mitigate or exacerbate tundra warming through changes in abiotic conditions of the understory environment, such as changes in snow and permafrost depth, nutrient availability, soil moisture and soil temperature (Sturm et al. 2001, Myers-Smith et al. 2011, Myers-Smith and Hik 2013, Zamin et al. 2014). However fewer studies have explored the effects of increased canopy formation on the performance of their dwarf shrub neighbours (Bråthen and Lortie 2015), and there is no consensus on anticipated responses. If predictions hold true that climate-growth sensitivity will be highest at the interface between tall and low-shrub tundra plant communities (Myers-Smith et al. 2015) where dwarf shrubs are ubiquitous (Grace et al. 2002), then a taller and more dense tree and tall-shrub canopy could result in a widespread reduction in understory light availability and/or soil resources for dwarf shrubs at these transition zones. For important northern ecosystem components such as dwarf berry-producing shrubs, increased competition for light and/or other resources could lead to allocation trade-offs, such as a less fruit production in favour of increased stem height or other growth traits (Weiner 2004), potentially changing the distribution and/or decreasing the availability and abundance of treeline and tundra fruit.

The berries produced by dwarf shrubs such as *Vaccinium* and *Empetrum* species serve as essential resources for wildlife and Indigenous people in the North, and their cultural, ecological and economic value has been well documented for circumboreal regions northward (Parlee et al. 2005, Poppel and Kruse 2009, Karst 2010). Declining access and availability of northern land-based foods such as berries is a matter of Arctic food security (Wheeler and von Braun 2013), and Indigenous knowledge holders and land managers from across the North American North have indicated widespread changes in dwarf berry shrub growth, fruit production and fruit quality, which they in part attribute to increased climate variability (Kellogg et al. 2010, Downing and Cuerrier 2011, Hupp et al. 2015). While we know that dwarf berry shrubs have an inherent rhythm to fruit production broadly attributed to plant neighbour effects, weather regimes and soil conditions (Shevtsova et al. 1995, Krebs et al. 2009, Holden et al. 2012), insight from gradient studies (Jentsch et al. 2009, Trant and Hermanutz 2014) and experimental warming studies (Anadon-Rosell et al. 2014) at treeline indicate that plant growth and reproductive responses are likely to be species- and context-specific. Therefore, a multi-species approach will be necessary to 1) distinguish which abiotic and biotic factors are important in driving circumpolar berry species response, and 2) support northern climate change adaptation response initiatives.

The ubiquity and persistence of dwarf berry shrubs across global treeline and tundra ecosystems is due in part to their propensity for clonal growth, longevity and phenotypic plasticity in growth form (De Kroon and Hutchings 1995). These persistence traits, which are often used as key predictors of climate-driven range shifts in canopy species (Estrada et al. 2016), will likely play an important role in determining the future impacts of warming on fruit production at treeline. For example, Parsons et al. (1994) showed that varying sensitivity of growth (biomass allocation) to environmental change (temperature, water and fertilizer) in four dwarf berry shrubs was attributed to differences in mode of lateral spread. Similarly, Shevtsova et al. (1995) showed that growth and reproduction of dwarf berry shrubs differentially respond to manipulated resource availability and neighbour presence, with negative growth responses in constrained prostrate growth habits. Although facilitation is thought to outweigh competition in northern ecosystems where species are under significant climate and resource stress (Brooker and Callaghan 1998, Wipf et al. 2006), alpine plant communities exhibit a gradient in stress, with competition often prevailing at lower elevations where conditions are less harsh, preventing upslope species from moving down the gradient (Choler et al. 2001). With that in mind, we anticipate that truly prostrate (i.e. without the physiological flexibility to grow upright) berry shrubs will exhibit higher trade-offs in fruit production under abiotic constraints of canopy than those with more flexible growth strategies who can better compete for aboveground resources at the leading edge of treeline.

In this study, we examine understory dynamics in treeline ecosystems by investigating the species-specific relationships between tree and shrub canopy structure (biotic) and near-ground microclimate (abiotic) on growth and fruit production of three circumpolar dwarf berry shrubs across the forest-tundra ecotone in Nain, Nunatsiavut, Labrador. Terrestrial ecosystems are undergoing significant environmental changes in Nain and other communities of eastern Sub-Arctic Canada associated with climate warming. These include but are not limited to tundra greening (Lévesque et al. 2012, Ropars et al. 2015), shifting species' (plant and animal) distributions and declining berry abundance and quality (Gerin-Lajoie et al. 2016), with significant impacts on subsistence resources (Downing and Cuerrier 2011, Cunsolo Willox et al. 2012).

The forest-tundra ecotone is an ideal location to study dwarf berry shrub performance as it allows us to capture phenotypic expression of each berry species along a natural gradient in plant distribution, and across a range of abiotic and biotic conditions (Pato and Ramón Obeso 2012). Our focal berry species include two evergreen [*Empetrum nigrum* L. (black crowberry) and *Vaccinium vitis-idaea* L. (mountain cranberry/lingonberry)] and one deciduous [*V. uliginosum* L. (alpine bilberry)] dwarf berry shrub common to treeline ecosystems globally. In Nain, Nunatsiavut, *E. nigrum* (paungaKutik [whole plant]; paungak [berry]), *V. vitis-idaea* (kimminaKutik [whole plant], kimminak [berry]) and *V. uliginosum* (kigutanginnaKutik [whole plant], kigutanginnak [berry]) are staple plants within the Nainimiut traditional food system with a variety of historic and current uses including using stems, leaves and fruit for food, medicine, and as combustibles (Clarke 2012).

These three species share many general life history characteristics common to clonal dwarf shrubs, yet they fundamentally differ in their mode and capacity for upright stem growth (Table 3.1; Figure 3.1). *Vaccinium uliginosum* grows both prostrate and upright due to its sympodial growth habit. Terminal buds produce flowers in the spring, while branching occurs from lateral buds (Jacquemart 1996). This results in a highly branched architecture with the ability to accrue significant height. The stems of *E. nigrum*, which have a creeping growth habit, elongate monopodially. However, the leading stems are densely branched and leafy, allowing intermediate levels of upright growth. This species is also known to be allelopathic (Bell and Tallis 1973). Although stem elongation occurs mono- and sympodially in *V. vitis-idaea*, its creeping growth form is highly prostrate with very limited capacity for upright growth (Ritchie 1955). All species can tolerate at least moderate amounts of shade; however, the species-specific trade-offs in growth and fruit production have not been explicitly explored at treeline in the context of food security for wildlife and Indigenous peoples of the North. Based on species' gradients in phenotypic plasticity, we predict that:

1. There will be a general increasing gradient in fruit production (FP) that corresponds to decreasing canopy structure and increasing light availability across the forest-tundra ecotone (Forest/low light/low FP< Forest-tundra transition/intermediate light/intermediate FP < Tundra/high light/high FP).
2. We will observe a growth-fruit production trade-off that will be stronger for truly prostrate berry shrubs with less capacity to compete for aboveground resources (V*accinium vitis-idaea* > *Empetrum nigrum* > *Vaccinium uliginosum*).

3. Microclimatic conditions (abiotic constraints) will have a stronger effect on the presence of fruit and extent of fruit production in truly prostrate growth forms vs. canopy structure (biotic interactions) for growth forms with greater capacity to compete for aboveground resources (*Vaccinium uliginosum* ~ Biotic > Abiotic; *Empetrum nigrum* ~ Biotic = Abiotic; *Vaccinium vitis-idaea* ~ Abiotic > Biotic).

3.2 Methods

3.2.1 Study site

Our study site is in Nain, Nunatsiavut (Labrador) (56°33 N, 61°41 W), which is the northeastern-most community in Sub-Arctic Canada representative of alpine treeline ecosystems (Fig. 3.2A). Nain has a distinctly maritime climate, with an average of 517.7 growing degree days above 5°C, and rainfall and snowfall amounts averaging 450.2 mm/year and 475.3 cm/year respectively. The mean annual temperature is -2.5°C with average daily maximums and minimums of 1.7 and -6.6°C respectively. In northern Labrador, the most recent decade (2001-2010) has warmed almost 1°C compared to the 1981-2010 Climate Normals period (Environment Canada 2015).

In Nain, the forest and treeline canopy are largely dominated by white spruce [*Picea glauca* Moench (Voss)], black spruce [*P. mariana* (Mill.) Britton, Sterns & Poggenb.], and eastern larch [*Larix laricina* (DuRoi) K. Koch], with balsam fir (*Abies balsamea* (L.) Mill) scattered throughout. Canopy-forming shrubs also persist throughout the forest-tundra ecotone, including dwarf birch (*Betula glandulosa* Michx.), green/mountain alder [*Alnus viridis* (Chaix) DC. ssp. *crispa* (Aiton) Turrill] and upright willows (*Salix* spp. L.).

3.2.2 Sampling design

To compare growth and productivity across the forest-tundra ecotone, we delineated four vegetation zones within the forest-tundra ecotone along an altitudinal gradient: forest (F), lower forest-tundra transition (FTL), upper forest-tundra transition (FTU) and low-shrub tundra (LST). These zones are classified by canopy structure (erect vs. prostrate growth form), composition (primarily tree vs. shrub species) and density (closed canopy vs. patchy and open), and loosely follow subzone definitions put forward by Scott (1995) (Fig. 3.2B). To quantify characteristics of the canopy, understory and near-ground microclimate across the forest-tundra ecotone, we established three 5 m x 50 m belt transects at north and south facing aspects for each of the four ecotonal zones (F, FTL, FTU and LST). LST was not represented on the north-facing slope, therefore N = 21 transects rather than 24 for all zone-aspect combinations. At each belt transect, quadrat locations were alternated upslope and downslope at 5m intervals (e.g. n=10 quadrats/transect). Canopy-forming species were sampled within 5 m x 5 m quadrats, and all understory species/microclimate within 1 m x 1 m quadrats, which were nested within the former. A complete schematic of our sampling design is depicted in Fig. 3.2B. Sampling took place from mid-July to mid August 2010.

Canopy structure was quantified by measuring the density (total number of trees/quadrat), height (m) and clonal area (where appropriate) of all trees and tall (canopy-forming) shrubs (alder, willow and dwarf birch). Clonal area was estimated by measuring the longest axis (length) and the associated perpendicular axis (width) of each clone. Clonal boundaries of tall shrubs were defined based on breaks in continuous cover. Understory plant community composition and structure was quantified by one individual visually estimating the percent cover of all vegetation (vascular and non-vascular) to the nearest percent (exceeding 100% based on multiple layers), and randomly selecting stems to measure height (cm) of all upright shrubs (n=3 stems/species). In the southwest quadrant of each 1m^2 quadrat (25 x 25 cm subplots), we counted the total number of flowers and fruits and flowers for each of our focal berry shrubs. Within the same 1m^2 quadrats, we quantified near-ground microclimate conditions by measuring ground and shrub level photosynthetically active radiation (PAR) (µmol/s/m^2; LI-COR 190 Quantum sensor and LI-250A Light meter, LI-COR, Lincoln, Nebraska, USA), soil temperature (^{0}C) and percent soil moisture of the organic soil horizon (Delta-T W.E.T. Sensor, Hoskin Scientific, Burlington, ON). Variability in daytime microclimate measures was reduced by sampling only during overcast conditions or days with clear sky, and between 10:00am and 2:00 pm.

We observed minimal and scattered evidence of herbivory from insect, small and/or large mammalian herbivores (such as rodents, moose and caribou) throughout our vegetation sampling. Therefore, herbivory was deemed an insignificant stressor on growth and fruit production across our forest-tundra ecotone. Salinity from ocean spray was also an insignificant factor, since transects were established approximately 2.3 km from the nearest shoreline.

3.2.3 Data summary

Tree and shrub canopy structure data (5m x 5m quadrats) were averaged at the plot level to estimate mean canopy height (m), total density (25m^{-2}) and mean clonal area (m^2/25m^2). From percent cover estimates in the understory (1m x 1m quadrats), we calculated plot-level total vegetation cover, canopy cover (total cover of all trees and upright shrubs), and total tree/shrub cover (total cover of all trees, upright and ground-surface shrubs). Average stem height (n=3 stems/species) and total cover was estimated for our three focal berry shrubs, and their upright neighbours (including dwarf birch). Preliminary measurements indicated that dwarf birch was the tallest and had the highest relative cover of all upright shrubs in the understory; therefore, we used average dwarf birch height (n=3 stems) as a surrogate for maximum shrub canopy height (cm) in the understory. Mean percent available PAR (relative PAR) was estimated by calculating the percentage between PAR measured at ground-level, and PAR measured at the level of the maximum shrub canopy layer (n=3 proportions/quadrat). Mean soil temperature (^{0}C) and mean soil moisture (%) were also calculated for each plot (n=3/quadrat/variable).

Given the remote nature of our study site, and the fact that our focal species have different flowering periods (Table 3.1), we were logistically constrained from obtaining fruit to flower ratios to determine fruit set for each species. Therefore, we estimated species-specific maximum potential fruit production (herein referred to as fruit production) by summing the total number of fruits and flowers present on each species during field work in July/Aug 2010 (mid-late summer in Nain). Counts were scaled up from 0.0625m^2 to estimate maximum fruit production/1m^2. This approach overestimates fruit production in favour of later flowering *V. vitis-idaea* (68.2% flowers), followed by *V. uliginosum* (43.0% flowers) and *E. nigrum* (0% flowers). Although we have no way of knowing whether flowers would in fact produce fruit, flower formation is a critical expression of reproductive effort, potential and output (Amasino et al. 2017). Since we are evaluating performance of each species individually, we propose that maximum fruit production is an acceptable response parameter to estimate abiotic and biotic constraints on reproductive output and interpret our results with this bias in mind.

3.2.4 Data analysis

Stand structure and community composition

To estimate the importance of microclimate in treeline plant community composition, abundance, and height, we tested the association between vegetation abundance, height and microclimate data using the Mantel test (Mantel and Valand 1970). We also explored the importance of zone and aspect in vegetation abundance and height by performing a multi-response permutation procedure (MRPP). To investigate patterns in growth of treeline vegetation in association with microclimatic conditions, we performed two ordinations (vegetation abundance and vegetation height) using non-metric multidimensional scaling (NMDS). Monte Carlo randomizations were used to test significance of variance explained in each dimension. We followed the iterative protocol outlined in Peck (2010) to specify initial analysis criteria (max. # axes = 4, max. # of iterations = 200, random starting coordinates, step length = 0.20, time = random # seed, 50 runs with real and randomized data) and to determine a final ordination solution.

We used Pearson product moment correlation coefficients (*r*-values) to interpret the strength and direction of relationships between vegetation/microclimatic conditions and ordination axes. Because of our large sample size (N=210), statistical significance was met with considerably low critical *r*-values (i.e. n=100, $p<0.05$ at r=0.197; Upton and Cook (2008)). Therefore we chose a conservative cut-off value of “r” (|0.400|) to interpret statistically significant relationships as suggested by McCune and Grace (2002). All multivariate procedures were run on untransformed data matrices (no significant outliers detected or removed) using Sorensen’s distance measure in PC-ORD version 6 (PCORD v.6; McCune and Grace 2002).

Fruit production

Unlike the plant growth traits measured as continuous variables in this study, the reproductive trait fruit production requires special attention. Fruit production data are discrete and naturally inflated by numerous but information rich zeros that represent biologically meaningful information about the presence vs. absence of flowers and fruit. As expected, we had a high frequency of true zero values in our estimates of fruit production for each species in this study (*E. nigrum* = 90%; *V. vitis-idaea* = 78%; Fig. 3). While generalized linear models are often used to model zero-inflated data (Zuur et al. 2007), traditional error families are not always suitable to overcome cases of high over-dispersion (Martin et al. 2005). As different biological processes may be driving the presence vs abundance of fruit in this study, we tested our predictions using a step-wise, two-part conditional generalized linear hurdle model, which utilizes different error distributions at each hurdle to investigate the effects of canopy structure (biotic interactions) and microclimate (abiotic conditions) on 1) the presence/absence of fruit (Binomial error and logit link), and 2) the extent of fruit production (Negative binomial error and log link) for each species (Martin et al. 2005, Zuur et al. 2012).

When we explored the variance of our growth and fruit production data within each zone-aspect combination, we found transect location to have minimal confounding effects on the distribution of our response and predictor variables within each zone.

Therefore, we treated quadrats (n=30) rather than transects (n=3) as replicates for each zone-aspect combination for all analyses (N=210). However, we noted that transect elevation, particularly at the south-facing aspect varied within some zones. Recognizing that elevation can drive differences in performance traits, we included elevation as a model term to account for this local variability.

Prior to model construction, collinearities between predictor variables were investigated by calculating Pearson product moment correlation coefficients (*r*-values) (Appendix 3.1). We observed significant (*p*-values < 0.001) collinearities among derived cover variables (total vegetation cover, canopy cover and total tree/shrub cover) and birch cover; therefore, we retained only total canopy cover to characterize the abundance of tree and tall shrub canopy. All global models of fruit production were specified using Type I sum of squares error structure. Predictor variables were ordered as follows: factors 'zone' and 'aspect' were entered first, followed by canopy structure ['canopy cover' (%), 'canopy density', 'mean canopy height' (m) and 'mean clonal area'), understory structure ('berry species cover (%)' and 'height (cm)', 'birch height (cm)'), and abiotic ('%PAR', '% Soil Moisture', 'Soil Temperature (°C)', and "Elevation (m)'] variables respectively. Interaction terms among covariates, growth traits and between biotic and abiotic parameters (i.e. 'height*PAR') were considered during the initial stages of model specification, however they were not included in final global models because our sample size, particularly among count models (zeros removed), could not support model convergence. A summary of all quantitative predictor variables with their means ± standard error is reported in Appendix 3.2. We fit fruit production models for each dwarf berry shrub using manual backwards selection by sequentially removing unimportant terms at $p > 0.05$. Models were run on unstandardized and standardized predictor variables. Our decision on alpha (5%) was unchanged between models, therefore we present only unstandardized versions of our final models. Variance inflation factors, residual and fitted values were examined at each step to evaluate influential points, error structure and independence. Goodness of fit was assessed by performing a chi-squared test based on the residual deviance and degrees of freedom. Models were run using package ‘MASS’ (Venables and Ripley 2002) and effects displays constructed in package ‘effects’ (Fox 2003) in R version 3.1.0 (R Core Team 2014). R-code is provided in Appendix 3.3.

3.3 Results

3.3.1 Stand structure and community composition

The results of the Mantel test indicate a highly significant positive correlation between vegetation abundance ($r = 0.227$; $t = 0.975$; $p < 0.001$), height ($r = 0.402$; $t = 0.252$; $p = 0.001$), and microclimatic factors, confirming that our abiotic parameters (PAR, soil moisture, temperature and elevation) are biologically meaningful correlates of plant community composition and structure across our study location. Pairwise comparisons indicate significant differences in vegetation abundance and height between zones, aspects and nearly all zone-aspect combinations (Appendix 3.4), suggesting that our data match the zonal delineations we set out to quantity across the forest-tundra transition, and that aspect should be considered as an important topographic variable in our models.

Our NMDS ordinations resulted in 2-dimensional solutions (Vegetation abundance: Stress=20.67; Final instability = 0.002 (Fig. 3.3A); Vegetation height: Stress

= 9.08; Final instability = < 0.001 (Fig. 3.3 B) with cumulative variance explained of 74.4% and 89.6% respectively. Both scatterplots (Fig. 3.3A,B) and associated species scores (Appendix 3.5, Appendix 3.6) indicate that the greatest differences in plots and species scores exist between the lower and upper forest-tundra transition zones along axis 1 (Fig. 3.3), and also between north and south facing aspects, but only for vegetation abundance along axis 2 (Fig. 3.3A). We also observed strong positive correlations between nearly all abiotic parameters (Elevation > PAR> Soil temperature) and plots above the lower forest-tundra transition zone for both ordinations, indicating that differences in vegetation abundance and height between the lower and upper forest-tundra transition are consistent with a gradient in increasing elevation, light and soil temperature from forest to tundra.

When we examine the abundance of dwarf berry shrubs (Fig. 3.3A; Appendix 3.5), only *Empetrum nigrum* exhibited a strong affinity to “zone” through significant correlations with forest and lower forest-tundra transition plots (axis 1; r = -0.726). Other significant forest and lower forest-tundra affiliates along axis 1 included typically boreal understory shrubs (*Rhododendron groenlandicum*, *Linnaea borealis*, *Cornus canadensis*), forbs (*Lycopodium* spp.), mosses (*Pleurozium schreberi*, *Dicranum* spp.) and lichens. The lack of significant correlation for *Vaccinium uliginosum* and *V. vitis-idaea* indicates that these species are not limited by environmental differences across the treeline ecotone. In the upper forest-tundra transition and low shrub tundra plots, positive correlations with axis 1 were observed for species with tundra affinity such as northern Labrador tea (*R. tomentosum*), sedges (*Carex* spp.) and lichens (*Cladina stellaris, C.* rangiferina, *Cetraria*/*Flavocetraria* spp, *Alectoria ochroleuca*). Although the variance explained was much weaker for axis 2 (15.9%), we observed a north-south gradient between *B. glandulosa* (r = -0.611) in south-facing plots and *Picea mariana* (r = 0.612) in north-facing plots, particularly among lower forest-tundra transition plots. These patterns indicate that aspect may be an important factor in growth response of canopy-forming species.

In contrast to berry species' abundances, all berry species' heights were significantly correlated with axis 1 (Fig. 3.3B; Appendix 3.6), with taller *E. nigrum* (r = -0.770) most strongly associated with tall canopy species (r = -0.871) and *Rhododendron groenlandicum* (r = -0.658) at the interface between forest and lower forest-tundra transition plots. *Vaccinium uliginosum* (r = -0.422) and *V. vitis-idaea* (r = -0.403) heights were most strongly associated with the tall-shrub *Betula glandulosa* (r = -0.540) and were tallest within lower forest-tundra transition plots. Heights of *R. tomentosum* (r = 0.473), a true tundra affiliate, exhibited the strongest correlations with upper forest-tundra transition plots. This observed gradient in height corresponds to a significant gradient in available light between the lower and upper forest-tundra transition, which is consistent with our predictions.

3.3.2 Fruit production

Our predicted trend of an increasing (upslope) gradient in fruit production was largely consistent with our results; however we observed the highest fruit production in the upper forest-tundra transition rather than the low shrub tundra, followed by lower forest-tundra transition, and almost a complete absence of fruit production in the forest zone (Fig. 3.4). Fruit production was generally highest for *V. uliginosum*, followed by *V. vitis-idaea* and *E. nigrum*, however these values were highly variable, owing in part to the high frequency of zero-values among berry species throughout the treeline (Fig. 3.5).

For *E. nigrum,* we found that the probability of fruit presence was higher on north vs south-facing aspects and under canopy <2m in height, however the maximum probability of fruit presence was less than 20% between predictor variables. Simply stated, there is a low probability of observing *E. nigrum* fruit across the forest-tundra ecotone across our study site (Table 3.2; Fig. 3.5a). In contrast, when we compare the significant factors affecting the probability of fruit production among *Vaccinium* species (Table 3.2; Fig. 3.5b-c), maximum probability of fruit presence is much higher (>80%) than for *E. nigrum*, and the same three factors are significant predictors of fruit presence for both *Vaccinium* species: “Zone” (FTL, FTU and LST), berry species “Cover (%)”, and “PAR (%)”. For *V. uliginosum*, there was a > 50% probability of fruit presence in the low shrub tundra and upper forest-tundra transition zones, whereas the maximum probability was slightly less than 30% for *V. vitis-idaea* in the upper forest-tundra transition. We observed a more gradual increase in probability of fruit presence for *V. uliginosum* cover values >20% vs. a more abrupt increase in fruit presence for *V. vitis-idaea* cover values >10%. This suggests that *V. uliginosum* has a more plastic growth-reproduction relationship than *V. vitis-idaea*, as predicted. Lastly, we observed a > 40% and > 20 % probability of *V. uliginosum* and *V. vitis-idaea* fruit presence respectively at PAR values ≥ 100% (Table 3.2; Figure 3.5b-c). Collectively, these results indicate that positive growth-reproduction relationships rather than trade-offs and available light are important predictors of fruit presence for *Vaccinium* species. Biotic interactions were less important than expected in predicting *V. uliginosum* fruit presence.

In contrast to the probability of fruit production, neither aspect nor zone were significant predictors of fruit production among berry species (Table 3.3; Fig. 3.6a-c). For *E. nigrum*, maximum fruit production (~125 fruit/m^2) was similarly predicted by low clonal area in canopy species, and under drier soil moisture conditions. Factors affecting extent of production were again consistent among *Vaccinium* spp. For *V. uliginosum*, the strongest positive predictors of fruit production included canopy cover >50%, *V. uliginosum* cover >40% and soil temperatures > 10°C respectively. For *V. vitis-idaea*, cover > 30%, soil temperatures > 10°C, and canopy density < 1 tree/tall-shrub/25m^2 were the strongest positive predictors of fruit production respectively (Table 3.3; Figure 3.6). These results emphasize positive growth-reproduction relationships over trade-offs, but this only appears to apply to *Vaccinium* spp. Unlike the trends we observed for probability of fruit presence, a combination of abiotic conditions and biotic interactions were significant predictors of fruit production for all berry species. This does not support our third prediction that abiotic constraints will have stronger effects on fruit production in prostrate growth forms vs. biotic interactions for growth forms with the capacity to compete for aboveground resources, such as light.

3.4 Discussion

Multi-species berry shrub performance (abundance, height and fruit production) differs among species at the interface between the lower and upper forest-tundra transition zone, with increasing elevation, light availability and soil temperature. Although we did not observe growth-reproduction trade-offs among species, characteristics of a closed canopy forest had consistent negative effects on the extent of fruit production for all berry species. Positive abundance-reproduction relationships were exhibited for both *Vaccinium* spp. across treeline, indicating the potential importance of plant abundance in reproduction allocation of these species. The relative importance of abiotic constraints vs. biotic interactions did not correlate to prostrate vs. upright growth forms in this study, however we identified that different abiotic and biotic factors are important in explaining the presence vs. extent of fruit production within and between species. This distinction could not have been made without the application of hurdle models. This study documents strong feedbacks between canopy structure and microclimate on fruit production at treeline, substantiating the claim that climate-induced canopy expansion, could reduce fruit production and availability throughout dwarf shrub tundra plant communities.

3.4.1 Trends in dwarf berry shrub performance across the forest-tundra ecotone

Our study confirms that dwarf berry shrubs and their tall-shrub neighbours exhibit plastic growth responses in abundance (*E. nigrum* and *B. glandulosa*) and height (all species) at treeline, with peak values being expressed between the forest (*E. nigrum*) and within the lower forest-tundra transition zone (*Vaccinium* spp. and *B. glandulosa*) (Fig 3.3). Our results are consistent with other ecotonal studies in eastern alpine Canada that found that community structure differs most prominently between the forest and forest-tundra zones (Harper et al. 2011, Trant et al. 2015) where canopy density is patchy and trees exhibit clonal growth to enable persistence. This shift in canopy architecture and distribution creates a heterogeneous light environment (Gratani 2014), which our dwarf berry shrubs responded to by increasing in height. The fact that we detected an abrupt aboveground resource shift in light and soil temperature between the lower and upper forest-tundra transition (Fig. 3.3) coinciding with a marked increase in fruit production (Fig. 3.4), indicates that the ecological constraints on fruit production are strongest between the forest and lower-forest tundra transition zones.

3.4.2 Factors affecting fruit production across the forest-tundra ecotone

Our models verified the observed trends that available light in the upper forest tundra transition zone (Fig. 3.5b-c) and warmer soil temperatures associated with canopy breakup (Fig. 3.6b-c) are strong positive predictors of fruit presence and abundance, respectively, in *Vaccinium* spp. We suspect this may be linked to habitat conditions in the upper ecotone that 1) support pollination of *Vaccinium* spp., and 2) protect plant reproductive structures from extreme climatic conditions. During field data collection we observed numerous bumblebees (*Bombus* spp.), which are efficient ``buzz`` pollinators of *Vaccinium* spp., foraging and returning to ground nests dispersed throughout the upper-forest tundra transition zone. This habitat is consistent with bumble bee nesting sites described by Packer et al. (2007). While Jacobs et al. (2014) documented relatively constant soil temperatures at alpine treeline in the Mealy Mountains, Labrador (Canada), soil temperatures in this study were nearly 1°C warmer in the upper versus the lower forest tundra transition zone, particularly at south facing aspects (Appendix 3.2). We propose that bee colonies benefit from direct sunlight and warmer soil surface temperatures in this zone, which is indirectly increasing foraging behaviour, pollinator attraction, and thus pollen transfer to *Vaccinium* spp. Pollinator activity is also supported by other co-occurring flowering species in this zone, such as *R. tomentosum*, which was a strong tundra affiliate both in abundance and height in the upper forest-tundra transition (Fig. 3.3). *Rhododendron* spp. are known to be pollinated by bumblebees (Kudo 1993), and provide important floral resources throughout the flowering period of tundra berry plants. These findings emphasize the importance of microclimate and exogenous factors on fruit production at treeline. Also, by virtue of lower elevation, dwarf shrubs in the upper forest-tundra are less exposed to wind and climatic stress than those in the low shrub tundra. Here, shrub architecture is low stature but still erect, which allows the shrub canopy to trap snow, thereby protecting perennating structures from potentially damaging disturbances such as wind, icing and winter warming events (Bokhorst et al. 2009, Bokhorst et al. 2011, Preece et al. 2012).

Fruit production in *E. nigrum* was much lower in comparison to *Vaccinium* spp.; however, fruit was more likely to occur on north vs. south facing slopes, and more abundant under drier soil conditions. At our treeline site, the north-facing aspect has a much steeper slope than the south-facing aspect, suggesting that fruit production in *E. nigrum* may benefit from well-drained soil conditions. Although fruit production and maximum shrub canopy (*B. glandulosa*) height were negatively correlated among species, this variable was not a significant predictor of fruit production across the forest-tundra ecotone.

Contrary to our prediction, we did not detect any significantly negative growth-fruit production relationships that would suggest allocation trade-offs within berry species. However, our lack of response does not mean that reproductive costs do not exist at treeline. While it`s true that light is a key abiotic constraint on plant growth at treeline, the relationship between light and reproductive structures is not well known (Xie et al. 2014). Similarly, more than one abiotic or biotic constraint can lead to reproductive costs. To overcome these complex in-situ interactions, Obeso (2002) explains that trade-offs in plants are best verified by manipulative experiments, where limiting conditions can be controlled, since many factors such as recent history, size and age differences will introduce variance in life history traits. If light is the most important constraint on fruit production, then it`s possible that other growth traits that relate more directly to plant survival and persistence under shade, such as specific leaf area or proportion of sun vs. shade leaves (Gratani 2014), may be more suitable to explore such trade-offs in nature.

Berry species cover exhibited a strong positive effect on both the presence and abundance of fruit for both *Vaccinium* spp., indicating there may be important thresholds between biomass, clonal size and reproduction at treeline. In a recent review of vegetative-reproductive relationships among herbaceous plants, Weiner et al. (2009) concluded that reproductive output of an individual is largely driven by its size, and that larger, long-lived plants often exhibit non-linear relationships in growth and reproduction, which is consistent with what we observed in this study, albeit among woody species. To better understand this relationship among dwarf berry shrubs, growth traits should reflect the plant's investment into prostrate vs upright growth, since persistence in the upper treeline is achieved by growing out rather than up. Future studies should also link clone size to pollinator visitation, since abundance-reproduction relationships could be linked to pollinator attraction (Dauber et al. 2010).

Our results did not support the prediction that fruit production in prostrate berry growth forms will be more constrained by abiotic conditions (microclimate) than biotic interactions (canopy structure) with upright growth forms such as *B. glandulosa*. While canopy structure variables had a stronger overall effect on fruit presence and extent of fruit production among berry species, all species were significantly influenced by microclimate, albeit different variables. Perhaps a more important finding was that the canopy and understory environment exhibited different constrains on when vs. how much flowers/fruit a berry plant produces. This distinction was made possible through hurdle models and emphasizes the importance of data rich zero-values in ecological datasets. Collectively, these finding confirm that canopy effects on fruit production are both direct and indirect; more study is required to establish the links between canopy effects, understory growth response, and sexual reproduction in various fruit producing species in the forest-tundra ecotone.

Other abiotic gradients in physical and chemical properties of soil not measured in this study could also be influencing observed trends in growth and fruit production among focal berry species. In the context of northern tree species, Lafleur et al. (2010) describes a variety of local soil properties (i.e. texture, porosity, moisture, nutrient availability (especially nitrogen and phosphorus) and permafrost dynamics) that individualistically constrain tree distribution at treeline. Coupled with variation in canopy litter input across treeline, direct and indirect effects of soil properties on dwarf berry shrub growth and fruit production are likely and require further investigation.

We did not consider the role of interspecific interactions among dwarf berry species on fruit production in the study. However, we know through neighbour removal and site manipulation experiments of our focal species (Shevtsova et al. 1995, Shevtsova et al. 1997) that growth and reproduction of prostrate growth-forms benefits from removal of upright neighbours, albeit with variable results under different site conditions. Therefore, it`s possible that interactions among berry species may vary from competitive to facilitative across the forest-tundra ecotone as biomass allocation shifts form upright to prostrate, with benefits to fruit production. This area requires further study, as facilitative interactions among berry shrubs could mediate, if only in the short term, the potential negative effects on fruit production of tall-shrub expansion into dwarf and low shrub tundra ecosystems.

3.4.3 Conclusions

Fruit production is a complex process to predict, particularly across resource gradients in a stressed environment. Our study has shown that canopy exerts significant effects on growth and fruit production in the understory at treeline. For dwarf berry shrubs, the effects of tall-shrub expansion into dwarf shrub ecosystems are perhaps more imminent than treeline expansion. Firstly, vegetative expansion of trees is slow, and expansion through seedling establishment can be mediated by poor seedbed suitability in the upper treeline (Wheeler et al. 2011, Dufour-Tremblay et al. 2012). Secondly, many tall-shrubs already persist within dwarf and low shrub tundra communities at low density and in prostrate form, therefore canopy formation can occur through infilling of existing individuals (Myers-Smith et al. 2011). For northern communities to mediate or adapt to changes in berry resources with future warming, subsequent studies should focus on the growth-reproduction relationships between dwarf berry shrubs and their tall-shrub neighbours (under experimental warming conditions) and explore possible strategies to actively managing shrub expansion to maintain or increase fruit production. These results will support adaptation response to changing berry resource availability under increasing climate stress.

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Zuur, A. F., A. A. Savaliev, and E. N. Ieno. 2012. Zero Inflated Models and Generalized Linear Mixed Models with R. Highland Statistics Ltd, Scotland, UK. 334p.

Table 3.1 Life history profile of three globally distributed dwarf berry shrubs among treeline and tundra ecosystems*.

Life history category	Traits	*Empetrum nigrum*	*Vaccinium uliginosum*	*Vaccinium vitis-idaea*
Growth	**Stem growth**	Monopodial - clonal	Sympodial -clonal	Monopodial and Sympodial - clonal
	Stem length (cm)	0-50	20-100	5-30
	Foliage	Evergreen	Deciduous	Evergreen
	Form	Prostrate	Erect or prostrate	Low dwarf-prostrate
	Branching	Creeping; Highly branched; densely leafy shoots	Low to high; annual shoots	Creeping
	Root system	Rhizomatous-extensive	Rhizomatous - extensive	Rhizomatous-extensive
Reproduction	**1° Propagation**	Vegetative	Vegetative	Vegetative
	Propagation method	Adventitious rooting of procumbent branches	Sprout or layer from rhizomes	Sprout or layer from rhizomes
	Flowering phenology	Early spring	Late spring-early/mid summer	Late spring-early summer
	Pollination	Wind/Insect (beetles)	Wind/Insect (bees, flies)	Insect/Wind (bees, flies)
Habitat	**Shade tolerance**	Moderate	Moderate-high	Moderate-high
	Soil Moisture	Well to poorly drained	Well to poorly drained	Well to poorly drained
	Mycorrhizal	Ericoid	Ericoid	Ericoid

*USDA, NRCS. 2015. The PLANTS Database (http://plants.usda.gov, 4 February 2015). National Plant Data Team, Greensboro, NC 27401-4901 USA.

USDA, NRCS. 2015. Fire Effects Information System (http://www.fs.fed.us/database/feis/HowToCite.html, 5 February 2015). U.S. Department of Agriculture, Forest Service, Rocky Mountains Research Station, Missoula Fire Sciences Laboratory

Table 3.2 Summary of statistics for binary (binomial error, logit link) generalized linear models predicting presence/absence of fruit production (total # fruits and flowers/m^2) of berry species across the forest-tundra ecotone. Coefficients are significant at $p < 0.05$.

Species	**Coefficients**	**Estimate**	**Std. Error**	**Z-Value**	**P-Value**	**Residual deviance/df**	**AIC**	**Chi-sq GOF**
Emni	Intercept	-0.79	0.34	-2.34	0.019	111.27/207	117.27	1.00
	Aspect[S]	-2.41	0.65	-3.71	<0.001			
	Canopy height	-0.30	0.13	-2.25	0.024			
Vaul	Intercept	-6.47	1.12	-5.78	<0.001	148.73/201	160.73	0.997
	Zone[FTL]	1.81	0.85	2.12	0.033			
	Zone[FTU]	3.22	0.83	3.86	<0.001			
	Zone[LST]	3.60	0.89	4.02	<0.001			
	Vaul cover	0.05	0.01	4.89	<0.001			
	PAR	0.03	0.01	2.87	0.004			
Vavi	Intercept	-5.71	1.07	-5.29	<0.001	136.31/201	148.31	0.999
	Zone[FTL]	1.22	0.88	1.39	0.164			
	Zone[FTU]	2.06	0.83	2.47	0.013			
	Zone[LST]	0.97	0.94	1.03	0.300			
	Vavi cover	0.15	0.04	4.07	<0.001			
	PAR	0.03	0.01	2.41	0.016			

Emni = *Empetrum nigrum*, Vaul = *Vaccinium uliginosum*, Vavi = *Vaccinium vitis-idaea*; F = Forest, FTL = Forest-tundra lower, FTU = Forest-tundra upper, LST = Lower shrub tundra; N = north, S = South.

Table 3.3 Summary of statistics for count (negative-binomial error, log link) generalized linear models predicting abundance of fruit (total # fruits and flowers/m^2) of berry species across the forest-tundra ecotone. Coefficients are significant at $p < 0.05$. Emni = *Empetrum nigrum*, Vaul = *Vaccinium uliginosum*, Vavi = *Vaccinium vitis-idaea*; F = forest, FTL = forest-tundra lower, FTU = forest-tundra upper, LST = lower shrub tundra; N = north, S = South.

Species	**Coefficients**	**Estimate**	**Std. Error**	**Z-Value**	**P-Value**	**Residual deviance/df**	**AIC**	**Chi-sq GOF**
Emni	Intercept	5.84	0.50	11.69	<0.001	22.07/18	227.43	0.228
	Clonal area	-0.01	0.00	-3.11	0.001			
	Soil moisture	-0.03	0.01	-2.21	0.027			
Vaul	Intercept	3.37	0.97	3.90	<0.001	87.41/72	1038.6	0.104
	Canopy cover	-0.01	0.00	-4.49	0.001			
	Vaul cover	0.02	0.00	3.37	0.001			
	Soil temp.	0.28	0.09	3.00	0.003			
Vavi	Intercept	-0.78	1.11	-0.70	0.480	49.22/41	517.07	0.177
	Canopy density	0.15	0.06	-2.41	0.015			
	Vavi cover	0.04	0.01	5.68	<0.001			
	Soil temp.	0.55	0.11	4.97	<0.001			

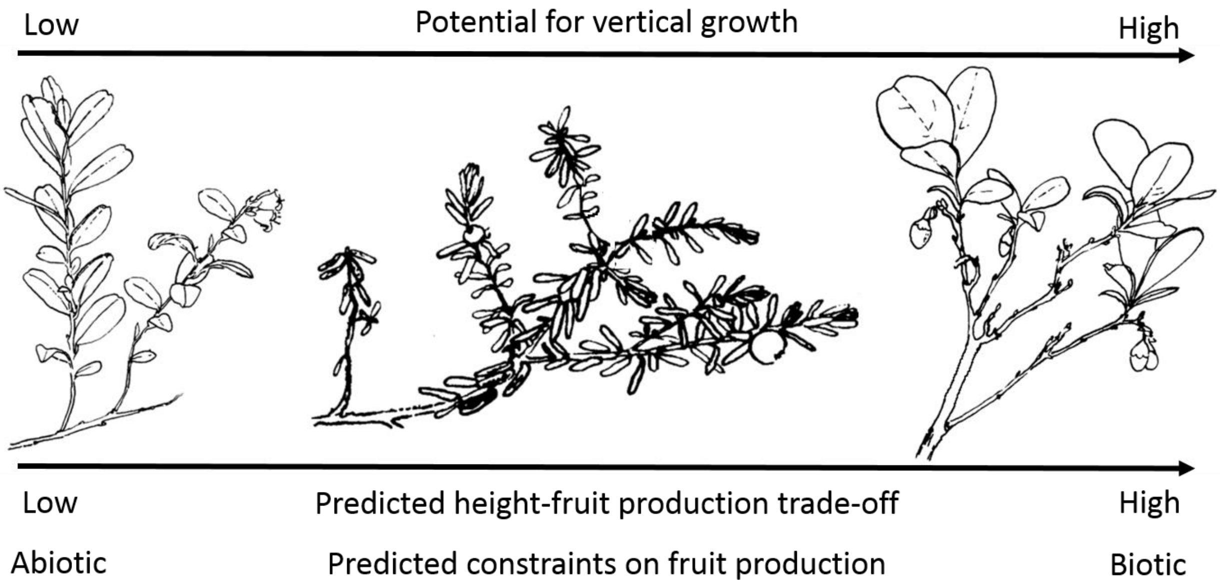

Fig. 3.1 Morphological diagram of dwarf berry shrubs studied in northern Labrador along a growth flexibility gradient. Left to right = *Vaccinium vitis-idaea*, *Empetrum nigrum* and *V. uliginosum*. Sketches are modified from Shevtsova et al. (1995).

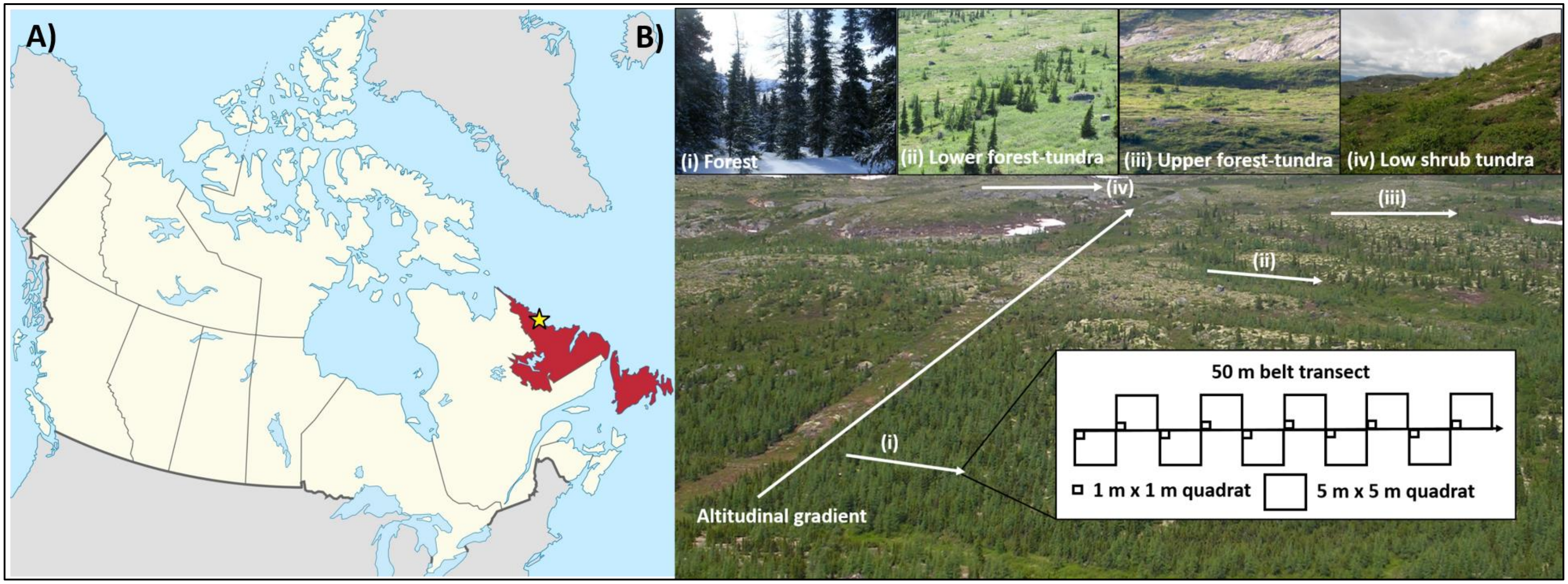

Fig. 3.2 A) Map indicating location of study site in Nain, Newfoundland and Labrador (NL), Canada; Nain is indicated by yellow star; white shading indicates Canadian boundaries; red shading indicates province of NL; map modified from www.wikipedia.org; B) Photographs and schematic illustrating sample location and design across the forest-tundra ecotone. The forest (i) is characterized by erect and dense tree growth, forming a closed canopy environment. In the lower forest-tundra transition (ii), canopy structure is open but with trees still growing in erect form. The upper forest-tundra transition (iii) has patchy tree cover with mostly prostrate growth form. The low shrub tundra (iv) is treeless with dwarf birch (*Betula glandulosa*), alder (*Alnus* spp.) and willow (*Salix* spp.) growing densely in prostrate form.

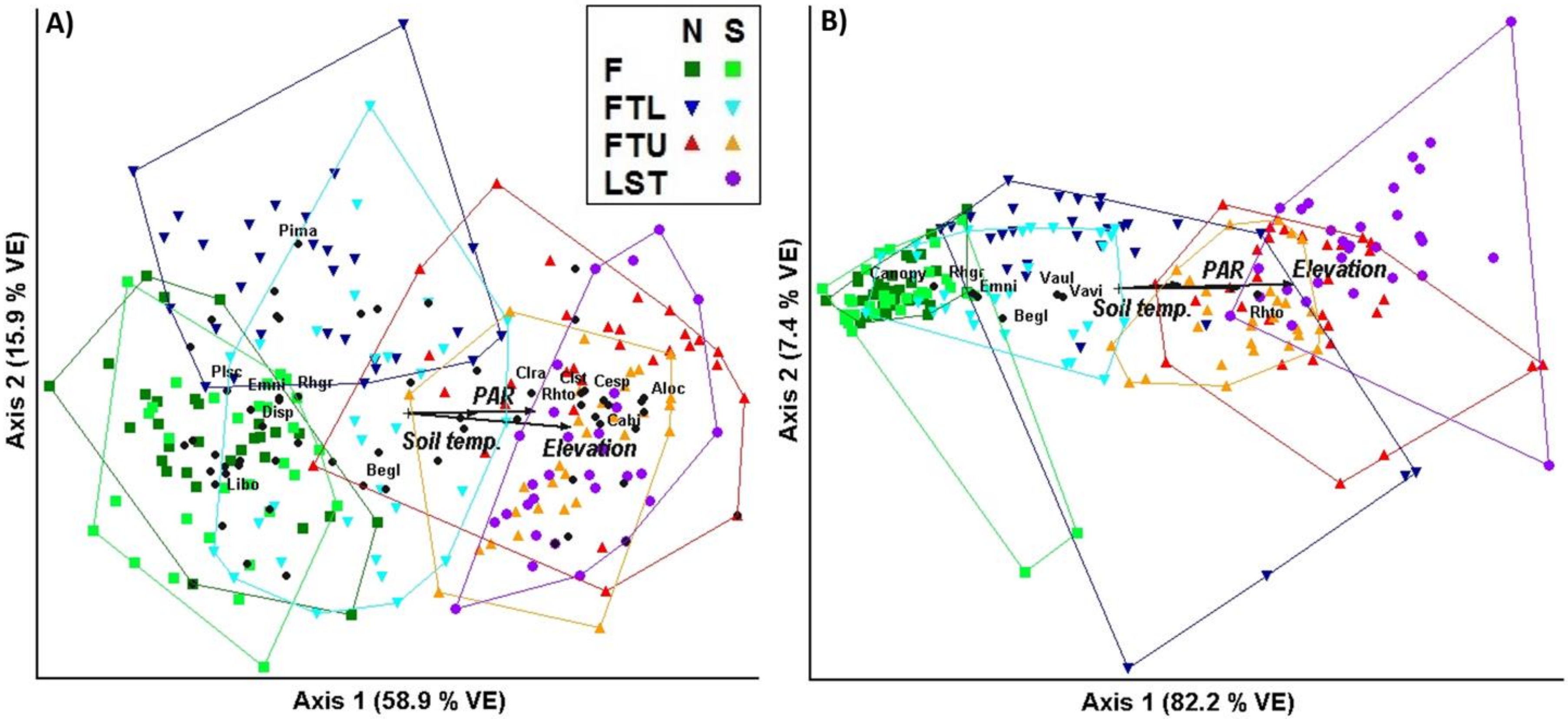
A)
N
S
F
FTL
FTU
LST
Pima
Plsc
Emni
Rhgr
Disp
Libo
Begl
Clra
Clst
Cesp
Rhto
Aloc
Cahi
PAR
Soil temp.
Elevation
Axis 2 (15.9 % VE)
Axis 1 (58.9 % VE)
B)
Canopy
Rhgr
Emni
Begl
Vaul
Vavi
PAR
Elevation
Soil temp.
Rhto
Axis 2 (7.4 % VE)
Axis 1 (82.2 % VE)

Fig. 3.3 Ordination scatterplots (NMDS with Sorensen's Distance) of vegetation abundance (A), vegetation height (B) and environmental correlations with axes 1 and 2. Sample zones across the forest-tundra ecotone are represented by unique symbols, aspect by colours and convex hulls by solid lines (which enclose points within a sample zone). Species are represented by ● symbol. All species with significant correlation coefficients are labelled (codes provided in Appendix S3). The direction and length of vectors indicate strength of correlations between environmental variables and ordination axes. NMDS ordination resulted in a 2-dimensional solutions (A) Stress=20.67; Final instability = 0.002; B) Stress = 9.08; Final instability = < 0.001) with cumulative variance explained of 74.4% and 89.6% respectively. F=forest, FTL=lower forest-tundra transition, FTU= upper forest-tundra transition, LST=low shrub tundra; N=North, S=South; PAR = Photosynthetic active radiation (%), Soil temp. = Soil temperature (°C); VE = Variance explained.

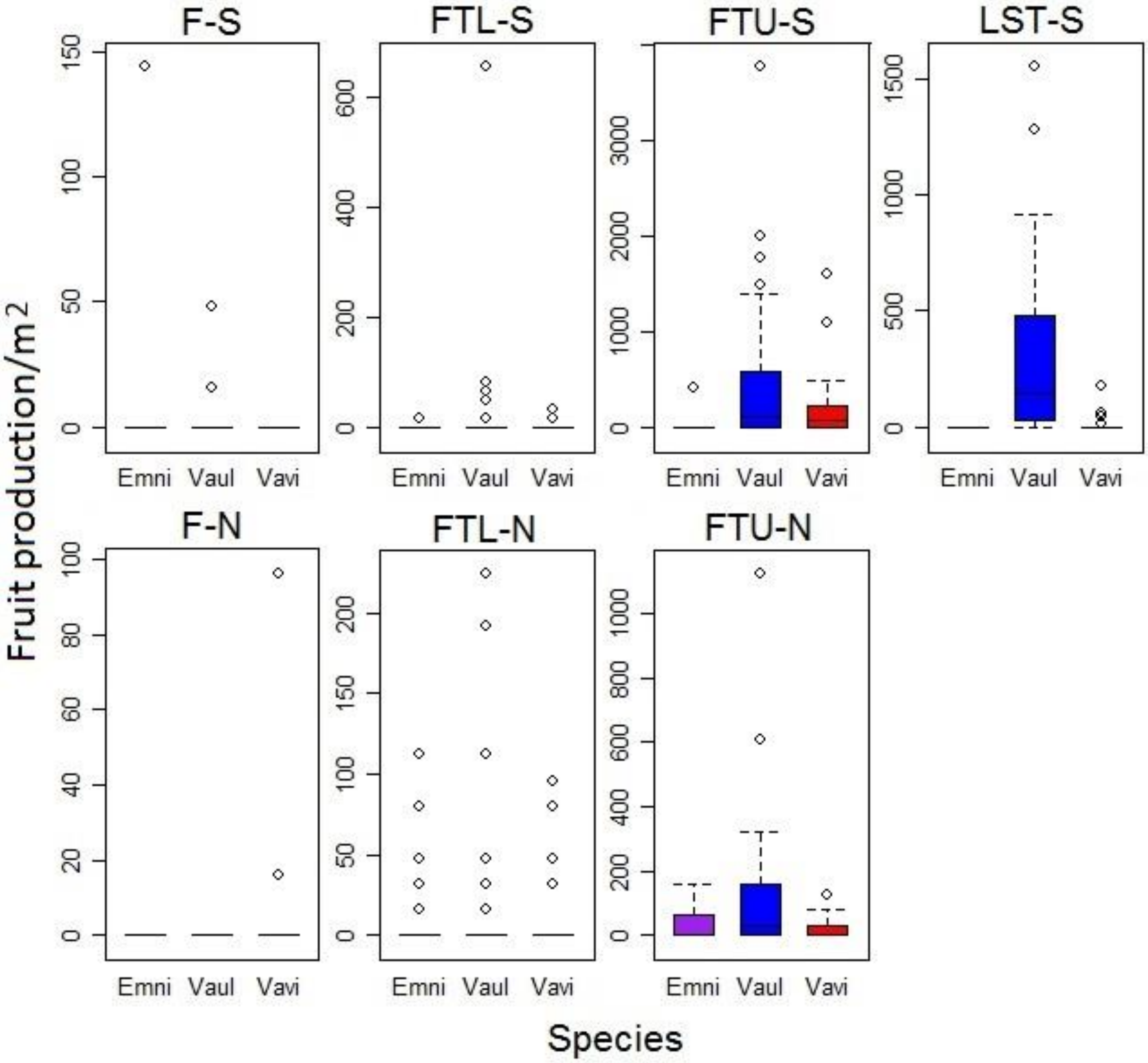

Fig. 3.4 Boxplots showing median, interquartile range, min/max and outliers for estimates of fruit production (total # fruits and flowers/m^2) for the three berry species studied within each Zone-Aspect combination. Emni = *Empetrum nigrum*, Vaul = *Vaccinium uliginosum*, Vavi = *Vaccinium vitis-idaea*; F = forest, FTL = forest-tundra lower, FTU = forest-tundra upper, LST = lower shrub tundra; N = north, S = South.

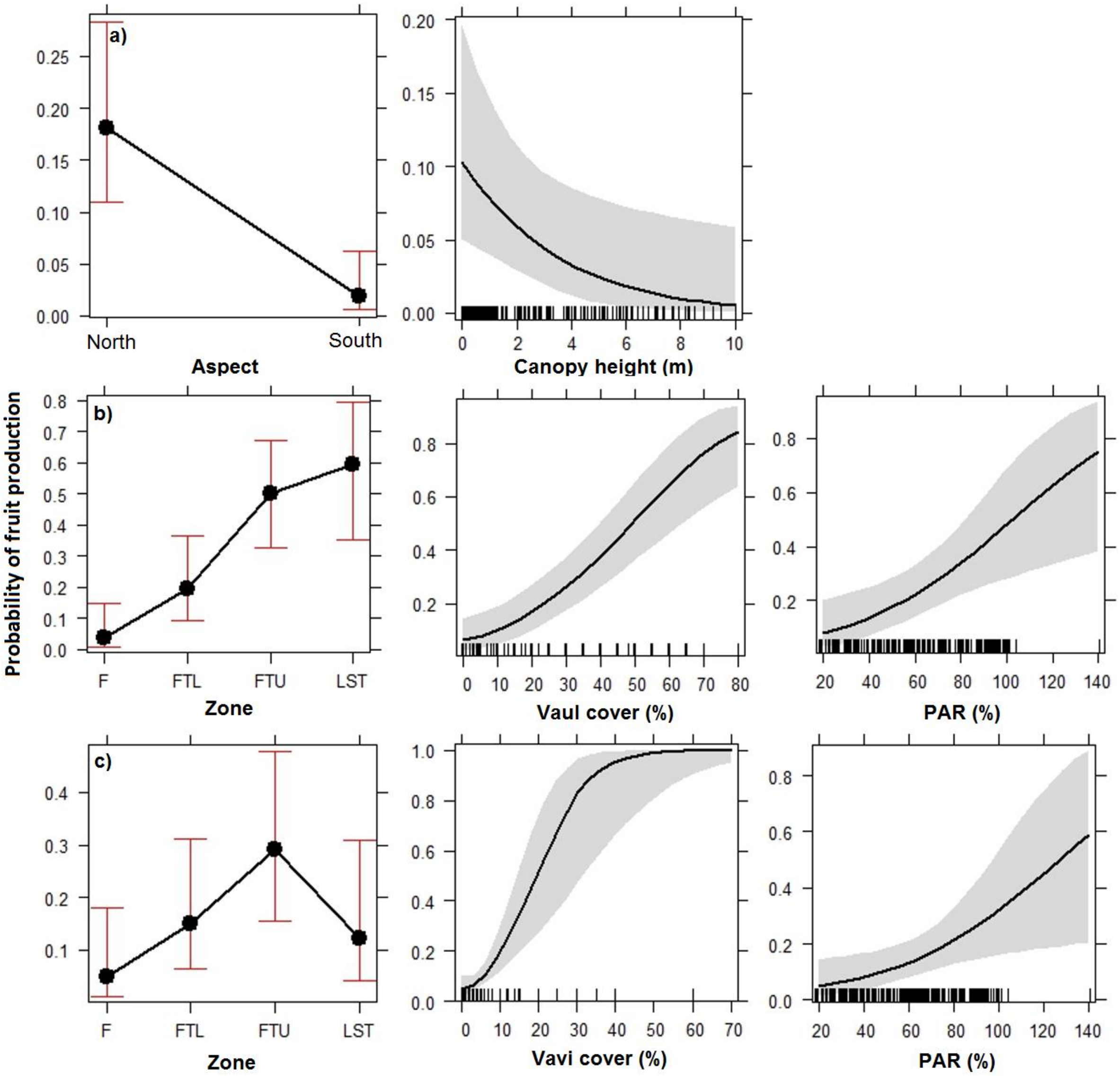

Fig. 3.5 Effects plots from binary logistic regression (logit link) indicating the magnitude and strength of significant parameter effects on the probability of fruit production in a) *Empetrum nigrum* (Emni), b) *Vaccinium uliginosum* (Vaul) and c) *Vaccinium vitis-idaea* (Vavi). Shaded areas represent 95% confidence intervals. F = forest, FTL = forest-tundra lower, FTU = forest-tundra upper, LST = lower shrub tundra; PAR = photosynthetically active radiation. Black lines along x-axis represent predictor observations and their raw values.

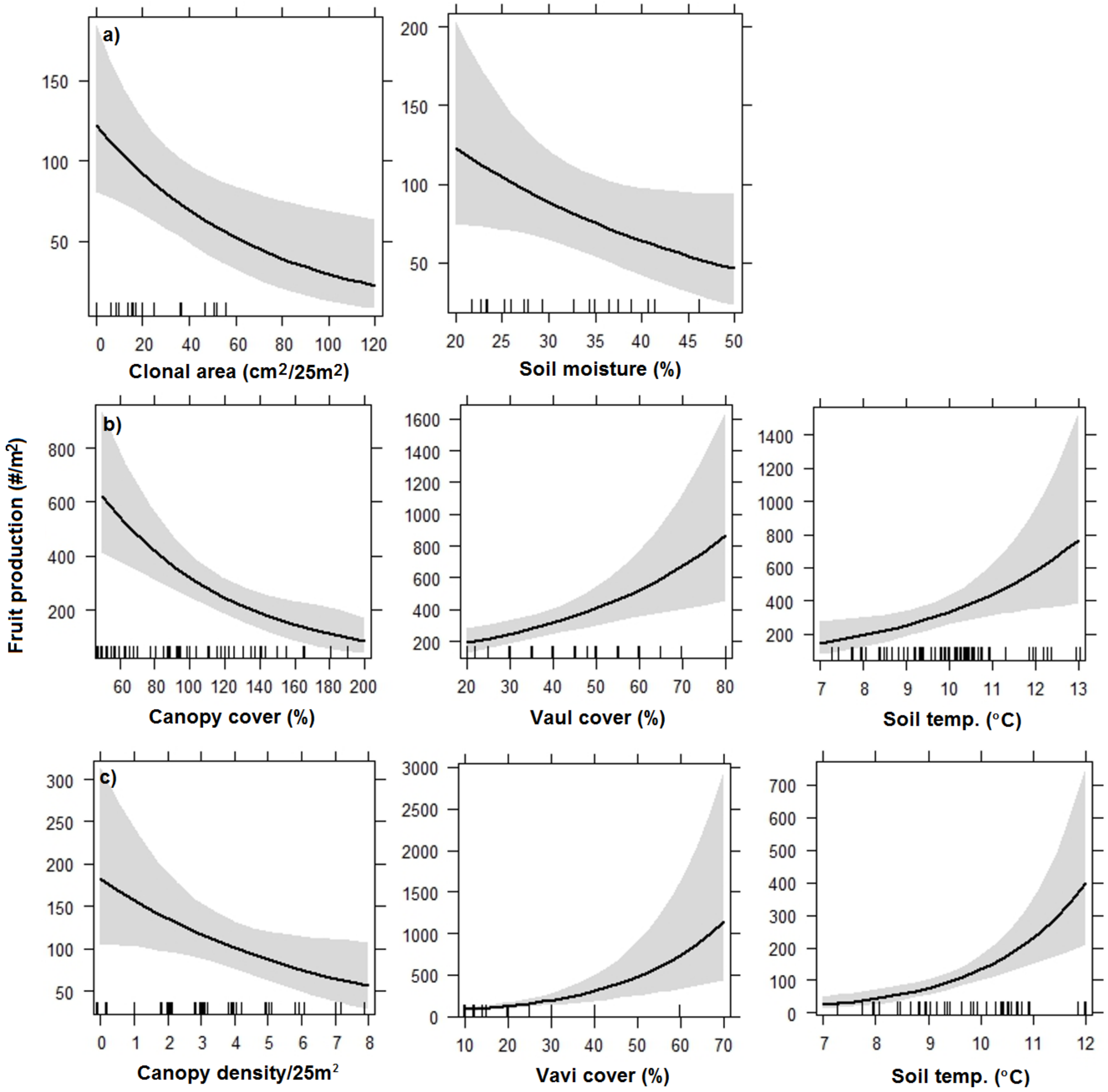

Fig. 3.6 Effects plots from generalized linear regression (negative binomial error, log link) indicating the magnitude and strength of significant parameter effects on extent of fruit production (total # fruits and flowers/m^2) in a) *Empetrum nigrum* (Emni), b) *Vaccinium uliginosum* (Vaul) and c) *Vaccinium vitis-idaea* (Vavi). Shaded areas represent 95% confidence intervals. F = forest, FTL = forest-tundra lower, FTU = forest-

tundra upper, LST = lower shrub tundra. Black lines along x-axis represent predictor observations and their raw values. Black lines along x-axis represent predictor observations and their raw values.

Appendix 3.1 Pearson product moment p-values (adjusted Holm's method) indicating significant correlations between vegetation response predictor variables at $p < 0.05$. Significant p-values of interest are in bold. x = Average, C = Cover, A=Area, Ht = Height, D = Density; Begl = *Betula glandulosa*, Emni = *Empetrum nigrum*, Vaul = *Vaccinium uliginosum*, Vavi = *Vaccinium vitis-idaea*.

	Canopy Cover	Tree/ ShrubC	Veg. Cover	X Clonal Area	XCanopy Height	Canopy Density	Begl Cover	Begl Height	Emni Cover	Emni Height	Vaul Cover	Vaul Height	Vavi Cover	Vavi Height
Canopy Cover	0.100	<0.001	**<0.001**	1.000	<0.001	<0.001	**<0.001**	<0.001	<0.001	<0.001	1.000	<0.001	1.000	<0.001
Tree/ ShrubC	**<0.001**	1.000	**<0.001**	1.000	<0.001	<0.001	**0.013**	<0.001	<0.001	<0.001	<0.001	1.000	1.000	<0.001
Veg. Cover	**<0.001**	**<0.001**	1.000	<0.001	<0.001	<0.001	**<0.001**	<0.001	<0.001	<0.001	0.144	0.002	1.000	<0.001
xClonal Area	1.000	1.000	1.000	0.910	0.910	<0.001	0.238	1.000	1.000	0.134	1.000	1.000	1.000	1.000
xCanopy Height	<0.001	<0.001	<0.001	0.910	1.000	<0.001	1.000	<0.001	<0.001	<0.001	0.144	<0.001	0.010	<0.001
Canopy Density	0.100	<0.001	<0.001	<0.001	<0.001	<0.001	1.000	0.115	<0.001	<0.001	1.000	1.000	1.000	0.005
Begl Cover	1.000	0.013	1.000	0.238	1.000	1.000	<0.001	<0.001	1.000	1.000	1.000	0.290	1.000	1.000
Begl Height	0.115	<0.001	<0.001	1.000	<0.001	0.011	<0.001	<0.001	<0.001	<0.001	1.000	<0.001	1.000	0.010
Emni Cover	<0.001	<0.001	<0.001	1.000	<0.001	0.010	1.000	0.005	<0.001	<0.001	0.120	0.002	1.000	<0.001
Emni Height	<0.001	<0.001	<0.001	0.134	<0.001	<0.001	1.000	<0.001	<0.001	1.000	<0.001	<0.001	0.238	<0.001
Vaul Cover	1.000	1.000	0.144	1.000	0.144	1.000	1.000	1.000	0.119	<0.001	<0.001	1.000	1.000	1.000
Vaul Height	<0.001	<0.001	0.002	1.000	<0.001	1.000	0.290	<0.001	0.002	<0.001	<0.001	1.000	1.000	0.021
Vavi Cover	1.000	1.000	1.000	1.000	0.010	1.000	1.000	1.000	1.000	0.238	1.000	1.000	1.000	1.000
Vavi Height	<0.001	<0.001	1.000	<0.001	<0.001	0.005	1.000	0.010	<0.001	<0.001	1.000	0.021	1.000	<0.001

Appendix 3.2 Mean and standard error of all canopy, understory and microclimatic predictor variables of fruit production measured across the forest-tundra ecotone. Fruit production estimates are presented in Fig. 3. Emni = *Empetrum nigrum*, Vaul = *Vaccinium uliginosum*, Vavi = *Vaccinium vitis-idaea,* Begl = *Betula glandulosa*; F=forest, FTL=forest-tundra lower, FTU=forest-tundra upper, LST=low shrub tundra.

	Aspect	North			South			
Category	Zone	F	FTL	FTU	F	FTL	FTU	LST
Canopy	Canopy height (m)	5.8 ± 0.3	1.5 ± 0.2	0.3 ± 0.0	5.6 ± 0.4	2.7 ± 0.3	0.4 ± 0.0	0.2 ± 0.0
	Canopy density (#/25m2)	9.2 ± 0.7	4.0 ± 0.5	3.1 ± 0.4	4.8 ± 0.6	3.7 ± 0.3	3.7 ± 0.2	3.4 ± 0.2
	Clonal area (cm2/25m2)	0 ± 0	49.1 ± 8.1	20.9 ± 3.1	0 ± 0	86.9 ± 13.1	51.8 ± 11.0	9.4 ± 1.0
	Canopy cover (%)	161.6 ± 6.7	153.5 ± 6.5	86.1 ± 8.7	145.9 ± 7.5	161.5 ± 6.5	90.0 ± 8.4	84.6 ± 6.3
Understory	Max. shrub canopy (Begl) height (cm)	46.2 ± 5.0	6.5 ± 3.0	10.9 ± 2.0	48.9 ± 5.6	41.3 ± 6.8	25.2 ± 3.2	3.6 ± 1.1
	Vaul cover (%)	19.1 ± 3.6	15.6 ± 3.3	23.0 ± 3.3	13.8 ± 3.2	38.1 ± 4.9	37.5 ± 3.8	38.3 ± 3.3
	Vaul height (cm)	12.7 ± 1.5	7.1 ± 1.1	4.6 ± 0.3	13.3 ± 1.6	16.4 ± 1.5	9.0 ± 0.9	6.2 ± 0.5
	Vavi cover (%)	4.9 ± 0.8	8.2 ± 1.2	7.0 ± 0.9	2.5 ± 0.4	4.1 ± 0.6	18.4 ± 3.7	4.4 ± 1.0
	Vavi height (cm)	7.5 ± 0.9	4.9 ± 0.2	3.2 ± 0.2	4.8 ± 0.7	4.7 ± 0.4	4.4 ± 0.4	2.0 ± 0.4
	Emni cover (%)	50.5 ± 4.2	43.7 ± 3.8	15.0 ± 3.5	47.7 ± 4.6	31.3 ± 4.5	2.9 ± 2.3	0.7 ± 0.4
	Emni height (cm)	22.6 ± 0.7	11.5 ± 0.9	3.8 ± 0.6	18.5 ± 1.5	10.9 ± 1.5	0.5 ± 0.3	0.1 ± 0.1
Microclimate	PAR (%)	61.7 ± 2.8	44.8 ± 3.5	83.2 ± 3.5	39.5 ± 3.6	35.9 ± 3.3	79.0 ± 4.2	77.2 ± 4.3
	Soil moisture (%)	28.3 ± 1.6	30.7 ± 1.6	36.1 ± 3.0	32.3 ± 3.5	34.0 ± 2.3	26.0 ± 0.8	29.6 ± 1.6
	Soil temperature (°C)	8.1 ± 0.1	8.6 ± 0.3	8.9 ± 0.2	8.2 ± 0.1	9.0 ± 0.2	10.2 ± 0.2	10.4 ± 0.1
	Elevation (m)	42.7 ± 5.0	86.3 ± 11.0	114.7 ± 3.7	89.3 ± 16.2	136 ± 21.0	175 ± 19.4	231.7 ± 14.1

Appendix 3.3 R code for generalized linear hurdle models using packages ‘MASS’ (Venables and Ripley 2002) and ‘effects’ (Fox 2003) in R version 3.1.0.

Hurdle Model: Step 1

```
>library(MASS)
>ModelName<glm(Y~X, family=binomial(logit), na.action=na.exclude, data=)
> summary(Modelname)
```

Hurdle Model: Step 2

```
>library(MASS)
> ModelName< glm.nb(Y~X, na.action=na.exclude, data=subset(, Y>0))
```

Effects displays:

```
>library(effects)
> plot(allEffects(model),rescale.axis=FALSE)
```

Goodness of Fit:

```
> 1 -pchisq(summary(model)$deviance,summary(model)$df.residual)
```

Appendix 3.4 MRPP statistics for pairwise comparisons of vegetation abundance and height between zones, aspects, and all zone-aspect combinations. All comparisons indicate significance at $p < 0.05$. T=Test statistic; A = Chance-corrected within-group agreement [1- (observed delta/expected delta)]; *p* = probability of smaller or equal delta. F=forest, FTL=forest-tundra lower, FTU=forest-tundra upper, LST=lower shrub tundra.

Groups	Pairwise Comparisons			Vegetation Abundance			Vegetation Height		
				T	A	*p*	T	A	*p*
Aspect	N	vs.	S	-20.430	0.030	<0.001	-3.72	0.010	0.010
Zone	F	vs.	FTL	-30.734	0.069	<0.001	-44.893	0.212	<0.001
	F	vs.	FTU	-67.013	0.207	<0.001	-77.257	0.459	<0.001
	F	vs.	LST	-50.826	0.199	<0.001	-58.416	0.480	<0.001
	FTL	vs.	FTU	-47.136	0.121	<0.001	-57.503	0.250	<0.001
	FTL	vs.	LST	-35.814	0.119	<0.001	-46.373	0.281	<0.001
	FTU	vs.	LST	-16.043	0.045	<0.001	-15.355	0.070	<0.001
Zone-Aspect	F-N	vs.	F-S	-11.504	0.053	<0.001	-1.421	0.012	0.090
	F-N	vs.	FTL-N	-25.010	0.132	<0.001	-31.010	0.315	<0.001
	F-N	vs.	FTL-S	-25.454	0.130	<0.001	-19.888	0.207	<0.001
	F-N	vs.	FTU-N	-34.366	0.245	<0.001	-39.377	0.497	<0.001
	F-N	vs.	FTU-S	-35.858	0.260	<0.001	-39.568	0.534	<0.001
	F-N	vs.	LST	-36.530	0.250	<0.001	-39.705	0.522	<0.001
	F-S	vs.	FTL-N	-20.560	0.097	<0.001	-27.453	0.256	<0.001
	F-S	vs.	FTL-S	-13.176	0.060	<0.001	-14.518	0.141	<0.001
	F-S	vs.	FTU-N	-32.693	0.212	<0.001	-37.442	0.435	<0.001
	F-S	vs.	FTU-S	-34.041	0.223	<0.001	-37.203	0.462	<0.001
	F-S	vs.	LST	-35.297	0.214	<0.001	-38.307	0.462	<0.001
	FTL-N	vs.	FTL-S	-16.133	0.079	<0.001	-7.9743	0.064	<0.001
	FTL-N	vs.	FTU-N	-26.419	0.160	<0.001	-25.756	0.229	<0.001
	FTL-N	vs.	FTU-S	-31.159	0.195	<0.001	-27.602	0.253	<0.001
	FTL-N	vs.	LST	-30.942	0.187	<0.001	-30.622	0.282	<0.001
	FTL-S	vs.	FTU-N	-25.877	0.142	<0.001	-34.104	0.328	<0.001
	FTL-S	vs.	FTU-S	-23.790	0.127	<0.001	-32.167	0.326	<0.001
	FTL-S	vs.	LST	-26.719	0.127	<0.001	-36.277	0.368	<0.001
	FTU-N	vs.	FTU-S	-11.745	0.054	<0.001	-10.327	0.071	<0.001
	FTU-N	vs.	LST	-16.726	0.073	<0.001	-7.859	0.053	<0.001
	FTU-S	vs.	LST	-13.651	0.057	<0.001	-19.311	0.140	<0.001

Appendix 3.5 Pearson correlation coefficients (r-values)[1] of vegetation abundance and environmental variables, sampled across the forest-tundra ecotone, with ordination axes. R-values indicate strength and direction of linear correlations between variables and ordination axes. Bold values indicate significance at $p<0.05$. Species codes are provided for those with significant correlation coefficients plotted on Fig. 3.3A.

Species	Axis 1	Axis 2	Species (cont'd)	Axis 1	Axis 2
Abies balsamea	-0.080	0.121	*Peltigera* spp.	-0.185	0.224
Alnus crispa	-0.057	-0.124	*Petasites* spp.	-0.085	-0.110
Alectoria nigricans	0.396	0.032	*Phyllodoce caerulea*	-0.287	0.144
Alectoria ochroleuca (Aloc)	**0.519**	0.054	*Picea glauca*	**-**0.370	-0.202
Arctous alpina	0.312	0.035	*Picea mariana* (Pima)	-0.240	**0.612**
Aulacomnium palustre	0.058	-0.084	*Pinguicula vulgaris*	-0.024	0.084
Bare ground	0.086	-0.083	*Pleurozium schreberi* (Plsc)	**-0.665**	0.139
Betula glandulosa (Begl)	-0.108	**-0.611**	*Poa* spp.	-0.076	-0.199
Carex bigelowii (Cabi)	**0.474**	-0.042	*Ptilium crista-castrensis*	-0.102	-0.036
Cetraria/Flavocetraria spp.(Cesp)	**0.517**	0.107	*Racomitrium lanuginosum*	0.153	-0.083
Chamaenerion angustifolium	-0.070	0.154	*Rhododendron groenlandicum* (Rhgr)	**-0.466**	0.113
Chamaenerion latifolium	-0.147	0.030	*Rhododendron lapponicum*	0.130	-0.167
Cladonia spp.	0.169	0.171	*Rhododendron tomentosum* (Rhto)	**0.623**	0.052
Cladina mitis	0.008	0.070	Rock	0.200	0.286
Cladina rangiferina (Clra)	**0.557**	0.148	*Rubus chamaemorus*	-0.120	0.145
Cladina stellaris (Clst)	**0.574**	0.113	*Salix planifolia/*spp.	-0.155	-0.178
Cornus canadensis	-0.378	-0.090	*Salix uva-ursi*	0.207	-0.137
Coptis trifolia	-0.303	-0.146	Sedge	0.092	0.000
Crust (lichen)	0.141	0.130	Soil	0.240	0.017
Diapensia lapponica	0.276	-0.032	*Solidago* spp.	-0.245	-0.244
Dicranum spp. (Disp)	**-0.435**	-0.062	*Sphagnum* spp.	-0.212	0.037
Empetrum nigrum (Emni)	**-0.726**	0.140	*Stereocaulon* spp.	0.180	-0.017
Equisetum spp.	-0.111	-0.171	*Lysimachia borealis*	-0.284	-0.138
Eriophorum spp.	0.125	-0.004	Unknown moss	0.003	0.073
Grass spp.	-0.330	-0.169	Unknown lichen	0.129	-0.066
Hylocomium splendens	-0.212	0.167	*Vaccinium caespitosum*	-0.280	-0.130
Kalmia polifolia	-0.113	-0.049	*Vaccinium uliginosum*	0.370	-0.168
Larix laricina	-0.313	0.013	*Vaccinium vitis-idaea*	0.206	-0.029

Linnaea borealis (Libo)	**-0.431**	-0.259	**Environmental Variables**	**Axis 1**	**Axis 2**
Litter	-0.346	-0.365	PAR (%)	**0.602**	0.072
Leafy liverwort	-0.054	0.309	Moisture (%)	0.113	0.039
Lycopodium spp.	-0.366	-0.216	TempGr (°C)	**0.444**	-0.013
Pedicularis spp.	0.037	-0.095	Elevation (m)	**0.683**	-0.202

[1] Critical r-value for significance at 5% (N=120) = 0.179 [Appendix III, Upton and Cook (2008)]. Therefore we chose a conservative r-value =|0.400| to estimate significance at 5% (N=210).

Appendix 3.6 Pearson correlation coefficients (r-values)[1] of vegetation height and environmental variables, sampled across the forest-tundra ecotone, with ordination axes. R-values indicate strength and direction of linear correlations between variables and ordination axes. Bold values indicate significance at *p*<0.05. Species codes are provided for those with significant correlation coefficients plotted on Fig. 3.3B.

Species	**Axis 1**	**Axis 2**	**Environmental Variables**	**Axis 1**	**Axis 2**
Vaccinium uliginosum (Vaul)	**-0.422**	-0.116	PAR (%)	**0.575**	0.036
Vaccinium vitis-idaea (Vavi)	**-0.403**	-0.167	Moisture (%)	0.115	0.025
Empetrum nigrum (Emni)	**-0.770**	-0.075	TempGr (°C)	**0.413**	0.120
Betula glandulosa (Begl)	**-0.540**	-0.378	Elevation (m)	**0.692**	0.107
Rhododendron groenlandicum (Rhgr)	**-0.658**	-0.100			
Rhododendron tomentosum (Rhto)	**0.473**	0.003			
Canopy (tree and tall shrub)	**-0.871**	0.026			

[1] Critical r-value for significance at 5% (N=120) = 0.179 (Appendix III, Upton and Cook (2008)). Therefore we chose a conservative r-value =|0.400| to estimate significance at 5% (N=210).

Chapter 4: Experimental warming effects on performance of culturally significant dwarf berry shrubs in eastern Low- and Sub-Arctic Canada.

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Abstract

Inuit Elders from across the Canadian Arctic have observed recent changes in the quantity and quality of berries, which is concerning given the high natural and cultural resource value of dwarf berry shrubs and their importance in tundra trophic dynamics. These observations concur with traditional and scientific knowledge that upright deciduous shrubs, especially *Betula* spp. in eastern Sub-Arctic regions are responding positively to climate warming by increasing in abundance and distribution (aka "shrubification"). Globally, greater dominance and distribution of upright deciduous shrubs could reduce the abundance, distribution and fruit availability of dwarf berry shrubs through shading effects on flower production/pollination success, resource competition, or changing abiotic conditions. Here, we examine the relationship between dwarf birch (*Betula glandulosa* Michx.) and three ericaceous culturally important dwarf berry shrubs [*Empetrum nigrum* L. (black crowberry), *Vaccinium vitis-idaea* L. (mountain cranberry/lingonberry) and *V. uliginosum* L. (alpine bilberry)] under short-term (2008/2009 to 2011) experimental warming conditions to determine the potential impacts on plant community attributes and fruit production. In two and three years of experimental warming, we demonstrated the responsiveness of *B. glandulosa* height to warming and showed that fruit production in prostrate berry shrubs (*V. vitis-idaea* and *E.*

nigrum) is more sensitive to warming and deciduous shrub height than berry species (*V. uliginosum*) with height plasticity. Warming reduced reproductive effort and success in *E. nigrum*, but mainly reproductive success in *V. vitis-idaea*. Divergent responses among prostrate berry shrubs to *B. glandulosa* height suggest a gradient in competitive and facilitative interactions among species. Fruit production varied greatly at the site and/or plot level, suggesting strong local drivers on fruit production across the eastern Low- and Sub-Arctic region. Future research and monitoring are required to determine the persistence of species-specific responses to warming and *B. glandulosa* growth traits over time.

Keywords: Eastern Low/Sub-Arctic Canada, experimental warming, dwarf berry shrubs, fruit production, shrubification, *Betula glandulosa*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea*, *Empetrum nigrum*

4.1 Introduction

In polar regions where climate variability and warming is changing at an unprecedented rate (Holland and Bitz 2003), the structure and function of tundra ecosystems is changing rapidly (Post et al. 2009). These changes are threatening global food security (Wheeler and von Braun 2013) primarily by limiting access and availability of animal and plant country foods (Ford 2009, Larsen et al. 2014). In the Canadian Arctic and Alaska, Inuit Elders and northerners have linked climate variability to changes in berry resources, such as decreases (and in some cases increases) in the growth, quantity and quality of culturally important dwarf berry species (Hupp et al. 2015, Gerin-Lajoie et al. 2016, Boulanger-Lapointe 2017). Berries are a staple country food among Inuit (Zutter 2009), and the process of picking, preparing and consuming tundra berries is vital to living Inuit culture (Zutter 2009, Downing and Cuerrier 2011, Cuerrier et al. 2015, Boulanger-Lapointe 2017). Dwarf berry shrubs also contribute to tundra ecosystem health and function by providing forage (Richardson et al. 2002, Cadieux et al. 2005, Christie et al. 2015) and habitat (Marcot et al. 2015) for vertebrate and invertebrate herbivores, supplying nutrients and storing carbon in above/below ground biomass and litter (Shaver et al. 1992, Grafius and Malanson 2015), and by retaining soil moisture and insulating winter soils through snow trapping (Myers-Smith et al. 2011), with direct links to permafrost and freeze-thaw cycles (Blok et al. 2010). Therefore, understanding how climate variability is driving changes in berry resources is critical to mitigating negative human health outcomes, and for anticipating feedbacks in tundra ecosystem processes that will inevitably influence tundra food-web dynamics.

Local observations from Inuit and First Nations communities in Canada demonstrate local changes in berry resources and climate (Cuerrier et al. 2015, Rapinski et al. 2017), yet the ecological mechanisms behind local drivers of fruit production have not been fully explored. Direct links between climate variables and dwarf berry shrub performance are more commonly explored in the literature. For example, extensive monitoring and manipulation of winter precipitation and temperature variables at tundra has shown that changes in snow depth and snowmelt timing (Wipf et al. 2009, Wipf 2010), and the occurrence of extreme winter warming, thawing and icing events (Bokhorst et al. 2009, Bokhorst et al. 2012, Preece et al. 2012, Preece and Phoenix 2014) can influence timing of leafout, extent of shoot elongation, bud develoment and fruit production in dwarf berry shrubs. However the direction of responses vary greatly among species. Simulated enhanced UV-B radiation and elevated CO_2 has also been shown to alter species-specific berry quality, abundance and seed germination (Gwynn-Jones et al. 2012).

Dwarf berry shrub performance may also be influenced by secondary effects of climate change, such as changing neighbour interactions with tundra canopy species. Since the 1980’s there has been documented increases in the growth (cover, abundance and/or biomass) and distribution of upright deciduous shrubs at multiple spatial scales throughout the treeline/tundra biome (Sturm et al. 2001, Tape et al. 2006, Tremblay et al. 2012, Myers-Smith et al. 2015). This response to climate warming is collectively referred to as “shrubification”, enabled through increased recruitment, vertical growth and asexual horizontal infilling (Myers-Smith et al. 2011). It is predicted that climate-growth sensitivity of upright deciduous shrubs will be highest at the interface between tall and low-shrub tundra plant communities (Myers-Smith et al. 2015). Dwarf berry shrubs are ubiquitous at this interface (Grace et al. 2002), emphasizing the importance of understanding tall shrub effects on dwarf berry shrub performance.

One obvious potential mechanism of change resulting from taller and more widespread deciduous shrub canopies at tundra is increased light competition with the understory. Lower light generally shifts resource allocation in plants from sexual reproduction (flower production) to asexual reproduction or persistence in the form of vertical/lateral growth and increased leaf area (Yang and Kim 2016). Fewer flowers can decrease pollination success, since fewer flowers will be less effective in attracting visitation from pollinators (Scaven and Rafferty 2013). Alternatively, tall-shrub canopies may ameliorate periods of temperature and moisture stress (Rixen et al. 2010, Bråthen and Lortie 2015), which is expected to increase with climate variability. In an assessment of factors driving *Betula glandulosa* Michx. densification in the eastern Sub-Arctic, Ropars et al. (2015) demonstrated that increased cover of *B. glandulosa* directly reduces the cover of neighbouring species, potentially through competitive interactions and/or changing local abiotic conditions. Given that cover (%) is a strong positive predictor of fruit production in dwarf berry shrubs at treeline (Chapter 3), significant increases in cover of neighbouring upright deciduous shrubs could displace or decrease berry shrub abundance and therefore fruit production.

In this study, we present a multi-species, multi-site analysis on the relationship between *B. glandulosa* cover and height and three culturally significant dwarf berry shrubs [*Vaccinium uliginosum* L. (bog bilberry/alpine blueberry), *V. vitis-idaea* L.

(redberry/lingonberry) and *Empetrum nigrum* L. (black crowberry)] under experimental warming conditions in Nunavik and Nunatsiavut, Canada. These regions are experiencing significant recent warming (Brown et al. 2012, Candlish et al. 2015) with well-documented positive influences on height and abundance of upright deciduous shrubs, especially *B. glandulosa* (Ropars and Boudreau 2012, Tremblay et al. 2012), and significant Inuit knowledge and observations of changes in plant and berry resources (Cuerrier et al. 2015, Gerin-Lajoie et al. 2016). Our goal is to improve our understanding of how warming and shrubification might influence growth and fruit production of dwarf berry shrubs to better inform natural/cultural resource management across the eastern Sub-Arctic region. We predict that:

1) Experimental warming will have positive effects on growth (cover and height) of *B. glandulosa* and other upright deciduous and tall shrubs, and negative effects on growth of ground dwelling vegetation. Dwarf berry shrubs, having varying life history strategies, will respond along a continuum, with less negative effects on growth of *V. uliginosum* followed by *E. nigrum* and *V. vitis-idaea* respectively;
2) Experimental warming and upright deciduous shrub growth (cover and height) will have negative effects on fruit production of dwarf berry shrubs; Fruit production in prostrate berry shrubs (*V. vitis-idaea* and *E. nigrum)* will be more affected than *V. uliginosum* given the latter species plasticity and capacity for upright growth.

4.2 Methods

4.2.1 Study Sites

Paired experimental warming and control plots were established in four locations and five sites across similar mesic site conditions in eastern Low and Sub-Arctic Canada, including: Kangiqsujuaq (Wakeham Bay; N=12) and Kangiqsualujjuaq (George River; N=14 and N=12), Nunavik, and Torr Bay (N=30) and Nain (N=9), Nunatsiavut (Fig. 4.1). Climate data from the most recent decade (2000-2009) indicates that mean annual temperature and mean total annual precipitation range from -1.8°C to -5.7°C and 449.4 mm to 882.5 mm across sites, with 318.3-684.1 growing degree above 5°C respectively (Table 4.1). Local climate station data near these locations indicate that the climate has experienced significant recent warming and increased precipitation, beginning in 1993 for Nunavik and Nunatsiavut (Brown et al. 2012, Ju and Masek 2016). Projected changes over these regions for the 2041-2070 period indicate that these climate trends are expected to continue, resulting in increased growing season length and growing degree days, a shortening of the snow and ice-cover season, as well as greater precipitation in the form of rain (Brown et al. 2012). These conditions are important drivers of tundra greening, suggesting continued shrub expansion throughout this region.

Four of five study sites are classified as Sub-Arctic, characterized by forest-tundra vegetation. However, experiments at these locations were established within mesic alpine tundra, where erect-dwarf shrub tundra vegetation dominates (Table 4.1). Across our study region, berry shrubs such as *Vaccinium* and *Empetrum* spp. are ubiquitous throughout the erect-dwarf shrub tundra plant community type, and they coexist at different densities and distributions with upright deciduous shrubs, primarily *B. glandulosa* but also *Salix* spp. (willow) and *Alnus* spp. (alder). Study sites were established in relatively homogeneous areas where shrub species coexist, and where treatment and control plots could be appropriately matched in terms of species composition, abundance and structure.

As presented in Chapter 3, our focal berry shrubs share many common life history traits characteristic of clonal dwarf shrubs, yet they differ greatly in their ability to accrue height based on their mode and capacity for stem growth. In terms of a structural hierarchy, *V. uliginosum* exhibits the greatest height capacity, with a sympodial (multiple lateral meristem) branching system where erect shoots can reach maximum heights of 70-100 cm (Jacquemart 1996). In contrast, *V. vitis-idaea* has the least height capacity. Although its stems elongate mono- (from a single terminal bud) and sympodially, this species is highly prostrate and reach maximum heights of 30 cm (Ritchie 1955). *Empetrum* nigrum falls between the two *Vaccinium* spp. As it elongates monopodially, it is densely branched and can reach maximum heights of up to 50 cm (Bell and Tallis 1973). Unlike the dwarf berry shrubs, *B. glandulosa* exhibits significant growth plasticity. In its prostrate form, erect stems range from 10-40 cm (Aiken et al. 2003), yet in treeline ecosystems or relief areas it can reach up to 2.5 m in height (Hermanutz et al. 1989).

4.2.2 Sample Design and Data Summary

The *in situ* warming experiments included in this study are part of the International Tundra Experiment (http://ibis.geog.ubc.ca/itex/), which uses a standardized passive warming design. Open-top warming chambers (herein referred to as OTC's) are constructed by fastening angled polycarbonate panels in a hexagonal design, which shelter vegetation from the wind and moderate diurnal heat loss, effectively raising the mean daily summer air temperature by 1-3°C (Molau 1997).

The standard ITEX plot size is 1m x 1m, and it is intended to monitor ecosystem-level change. We reduced our plot size to 70 cm x 70 cm to specifically track berry shrub performance at the plant community level. Experiments were established in 2008 (Nunavik) and 2009 (Nunatsiavut) and resampled after 2 and 3 years of passive warming in 2011. The technique used to quantify species composition, abundance and height in this study was through point-framing following the CANTTEX protocol (http://ipytundra.ca/sites/default/files/CiCAT%20point-framing%20protocol.pdf). However, there was some variation in sample intensity, which is summarized for all sites in Appendix 4.1. To account for different point frame sample intensities (# hits/plot) among sites and between years, we standardized point frame data by calculating the % cover (C) of individual species k (C_k) as:

$$C_k = (y_k / Y_K)*100$$

Where y represents the total number of hits for species k, and Y represents the total number of hits for all species (K) in a plot. Species-level data were pooled by vegetation lifeforms to obtain plot-level estimates of cover for the following plant functional groups: shrubs (all, deciduous and evergreen), forbs, graminoids, mosses and lichens. Height of all species (to the nearest 0.5 cm) was recorded at each point frame hit, and individual estimates were averaged to obtain a mean height (cm) for all species in each plot. We used *B. glandulosa* as a proxy for the upright deciduous shrub canopy layer across sites because it was the tallest, most dominant and frequently occurring upright deciduous shrub among sites.

We harvested the berries of our three target species at the end of each growing season across sites to quantify the effects of passive warming, year sampled and vegetation change on dwarf shrub fruit production within our plots. We standardized these data by scaling up our estimates of fruit production to total #fruit/species/m^2 (where necessary) because fruit were also harvested at different sample intensities among sites and between years (Appendix 4.1).

The nature and duration of plot-level climate monitoring (air/soil temperature, soil moisture, photosynthetically active radiation (PAR)) varied greatly among sites in this study, therefore we utilized local climate station data available through the Environment Canada Weather Archive to examine local variation in climate variables and their effects on vegetation (http://climate.weather.gc.ca/historical_data/search_historic_data_e.html). We summarized daily and monthly temperature data to calculate temperature-based variables that are important for growth and flower production as local and gridded precipitation records were absent for Nunavik communities over the sample period in this study (2008-2011). Data included mean annual, summer (June-July-August) and winter (December-January-February) temperature (°C), and the annual sum of growing (>5°C), freezing (<0°C) and thawing (>0°C) degree days.

4.2.3 Data Analysis

Community and dwarf berry shrub performance

Our primary response variable, fruit production (#fruit/m^2), contains many biologically meaningful zero values that “count” the occurrences of when fruit is present vs. absent for a given species. These zero values strongly skew the distribution of observations, making it difficult to model the data using traditional approaches (i.e. general linear models) based on the normal error distribution (Zuur et al. 2007). Zero-inflation can also occur with positive continuous data when attributes of a species are either very low or not present, as is often the case with abundance data (Warton 2005). In this study, a value of zero or very low cover (%) reflects meaningful plot-level variation on the presence/absence of certain vegetation lifeforms, particularly across sites. To account for these important characteristics in fruit production and functional group cover estimates, we use a two-part conditional hurdle model, which addresses the high occurrence of zeros by first estimating the probability that fruit and/or a functional group is present (Bernoulli distribution), and then if/when present, estimating the extent of fruit production and/or functional group cover using a different error distribution (fruit production = negative-binomial; functional group cover = gamma or Gaussian) (Martin et al. 2005, Zuur et al. 2012). To account for repeated measurements of the same sites and plots at multiple time-points, we used generalized linear mixed-effects models, with random intercept and fixed slopes for plots nested across our sites. This approach assumes similar baseline conditions across sites, such that our fixed effects will respond the same across our random subject groupings in the following form:

$$Y \sim (1|Site/PlotID) + X_1 + X_2 + X_x + (X_1 * X_x)$$

Where ‘Y’ = response, ‘1| Site/PlotID’ = random effect term for PlotID nested within Sites, ‘$X_{1\text{-}x}$’ = fixed effect predictors variables, and ‘$(X_1 * X_x)$’ = fixed effect interaction terms (Bates et al. 2015).

Prior to model selection, collinearities between predictor variables were investigated by calculating Pearson product moment correlation coefficients (*r*-values). We found strong correlations between seasonal temperature and degree day variables, and therefore included only summer (JJA) and winter (DJF) temperature (°C) as climate predictors (Appendix 4.2). We used a backwards selection strategy starting with a saturated mixed-effect model that included all possible random and fixed effects, and sequentially removed random and then fixed effects terms at $p > 0.1$ until we arrived at our final model (Zuur 2009, Elmendorf et al. 2011). Random effect terms were only removed when their variance approximated zero. Our decision on alpha ($p > 0.1$) was unchanged for standardized predictor variables; therefore, we present only unstandardized versions of our final models. Interaction terms among random/fixed factors, growth traits and climate variables (i.e., 'height*JJATemp') were considered during the initial stages of model specification, however we found that our sample size, particularly among count models (zeros removed), could not support inclusion of multiple interaction terms. Therefore, only fixed effect (i.e. 'Treatment*Year' and 'berry species cover*height') interactions were considered during model selection. Variance inflation factors, residual and fitted values were examined at each step to evaluate influential points, error structure and independence. Outliers were removed in only a few cases (response = fruit production; count models) where it dramatically improved model fit and enabled model convergence. Predictor variables were ordered as follows: random ('Site/PlotID') then fixed factors ('Treatment' and 'Year') followed by fixed factor interactions ('Treatment*Year'). All global models were specified using Type I sum of squares error structure.

Our modelling approach was to first examine the effects of our random and fixed factors on plant functional group cover and focal species' growth traits independently. Functional groups included shrubs (all), deciduous and evergreen shrubs, forbs, graminoids, mosses and lichens. Growth traits included cover and height of dwarf birch and our three focal berry species. Fruit production models were then specified to include random and fixed factors (as described above), plus fixed-effect terms for understory structure ('berry species cover (%) and height (cm)', '*B. glandulosa* cover and height (cm)'), within-species height-cover interactions, and local climate ('JJA' and 'DJF' temperature (°C)). In the first round of model selection, the factor 'Time' contained two baseline levels (2008 and 2009) to account for the difference in when experiments were established compared to the resample period (2011). In all candidate models, we found no significant difference between the baseline factor levels, and therefore proceeded with model selection based on pooled baseline data (2008/2009).

All generalized linear mixed hurdle models were analyzed in R version 3.3.0 (R Core Team 2016) using packages 'MASS' (Venables and Ripley 2002), lme4 (Bates et al. 2015) and glmmADMB (Bolker et al. 2013). Effects displays were constructed using package 'effects' (Fox 2003). R-code is provided in Appendix 4.3.

4.3 Results

4.3.1 Growth traits

Nearly all plant functional groups (5/7) exhibited significant changes in cover (%) over time in this study, but no change was detected due to experimental warming. Significant changes included increases in cover (%) of deciduous shrubs and forbs, and decreases in evergreen shrubs, graminoids and mosses (Table 4.2). *Betula glandulosa*, the dominant upright deciduous shrub across sites, exhibited a positive and significant increase in cover (%) over time, and a positive and significant increase in height (cm) with experimental warming over time (Table 4.2; Fig. 4.2). All focal berry shrubs exhibited significant changes in growth traits over time, but not due to experimental warming. While height significantly increased for all species, cover (%) response varied. *Vaccinium uliginosum* cover (%) increased with time, whereas *V. vitis-idaea* decreased. Changes in *E. nigrum* cover (%) were not significant (Table 4.2).

4.3.2 Fruit production

The distribution of raw fruit production data shows that the occurrence and extent of fruit was highly variable between years and treatments for all species (Fig. 4.3). Among our focal berry shrubs, *V. uliginosum* was the only species to demonstrate an increase in probability of fruit presence over time, irrespective of experimental warming (Table 4.3a; Fig 4.4-1d). Fruit presence in *V. uliginosum* was also positively predicted by its growth traits, with an 80 % probability of fruit presence when cover and height were > than 30 % and 12 cm respectively (Table 4.3a; Fig 4.4-1a-b). *Vaccinium uliginosum* cover (%) was the only significant predictor of fruit extent, with maximum fruit production values when cover was greater than 40-50 % (Table 4.3a; Fig 4.4-2a). We found no significant effect of experimental warming on this species. Colder rather than warmer mean summer temperatures were better predictors of fruit presence in this species, with 75 % probability of fruit production achieved at mean summer temperatures < 6 °C. Variance estimates > 0 for random effects terms (especially ‘Plot ID’) in both models indicate that fruit production varies at the local level for this species (Table 4.3a).

In *E. nigrum* (Table 4.3b), we observed a significant negative effect of experimental warming on the presence of fruit (Fig. 4.5-1f), and to a lesser extent on the amount of fruit produced (Fig. 4.5-2b). The extent of fruit production also decreased with time (Fig. 4.5-2c), with a decrease in more than 150 fruit/m^2 in 2011 compared to 2008/2009. Maximum *B. glandulosa* height was also an important negative predictor of fruit presence, with < 20 % probability of *E. nigrum* fruit presence when *B. glandulosa* was ≥ 20 cm tall (Fig. 4.5-1c). Like *V. uliginosum, E. nigrum* biomass was a positive predictor of fruit presence, with 80 % probability of fruit presence when cover and height were > than 40 % and 10 cm respectively (Fig. 4.5-1a-b). Cover was also a weak positive predictor of fruit extent (Fig. 4.5-2b). In contrast to *V. uliginosum*, warmer mean summer and winter temperatures improved the probability of fruit presence in *E. nigrum* (Fig. 4.5-1d-e). Variance estimates approximated zero for all but one random effect term (Step 2, 'Plot ID', Table 4.3b), indicating that *E. nigrum* fruit production is robust to site and plot level variation.

In both steps of hurdle modelling for *V. vitis-idaea,* high variance estimates for 'Site' and 'Plot ID' indicate that fruit production in this species was strongly influenced by local effects (Table 4.3c). Even though fruit occurrence was higher in experimental warming plots and in 2011, we observed a significant negative interaction effect between time and experimental warming. Therefore, among experimental warming plots only, the occurrence of *V. vitis-idaea* fruit decreased over time (Fig. 4.6-1b). Unlike fruit occurrence, the extent of fruit production significantly declined over time (Fig. 4.6-2d) and to a lesser extent with experimental warming (Fig. 4.6-2c). Consistent with the other berry species, *V. vitis-idaea* cover was a significant positive predictor of fruit occurrence

(90 % probability at ≥ 25 % cover) and fruit extent (> 150 fruit/m^2 at ≥ 32 % cover) (Fig. 4.6-1a,2a). We also observed a weak yet significant positive effect of maximum *B. glandulosa* height on *V. vitis-idaea* fruit extent (Fig. 4.6-2b).

4.4 Discussion

In just two and three years of experimental warming, we demonstrated the responsiveness of *B. glandulosa* height to warming and showed that fruit production in primarily prostrate berry shrubs (*V. vitis-idaea* and *E. nigrum*) is more sensitive to warming and deciduous shrub height than berry species (*V. uliginosum*) with the capacity for upright growth. Fruit production varied greatly at the site and/or plot level, suggesting strong local drivers on fruit production across the eastern Low and Sub-Arctic region, especially for *V. vitis-idaea*. Collectively, our study demonstrates the potential for future warming and shrubification to constrain fruit production of some culturally important prostrate berry shrubs at the regional scale.

4.4.1 Growth traits

Contrary to our first prediction, growth traits in plant functional groups (cover) and of our focal berry species (cover and height) were weakly affected by experimental warming in this study. We suggest a few possible reasons for this result. Although our experiments were established in relatively homogeneous mesic low shrub tundra communities, we observed significant variation in growth traits at the site and plot level (Table 4.2), indicating proportions of species may have differed at OTC establishment. Thus, two and three years of experimental warming may have been insufficient to overcome initial differences in plot characteristics. Inclusion of local topo-edaphic variables to account for plot and site level variation may have improved our detection of warming effects, as we know that functional group responses to warming are strongly influenced by plot and site-level moisture and productivity (Elmendorf et al. 2012). Nevertheless, *B. glandulosa* height responded positively to experimental warming in this study. This result is consistent with recent global syntheses efforts showing that plant height, especially among upright deciduous shrubs, is highly responsive to short and long-term warming across the tundra biome (Myers-Smith et al. 2015, Bjorkman et al. 2018).

The rate of background warming and climate variability across Nunavik and Nunatsiavut is reaching unprecedented levels (Brown et al. 2012, Finnis and Bell 2015, Bush and Lemmen 2019), which could be driving the significant growth signals we observed over two and three years for nearly all functional groups and focal species (Table 4.2). If we assume this to be true, our results on functional group cover, upright deciduous shrubs and berry species growth traits (especially height) closely align with ITEX syntheses studies, demonstrating that vascular plants increase, and non-vascular plants decrease with experimental warming (Elmendorf et al. 2011). One notable exception is that evergreen shrub cover decreased (albeit marginally) rather than increased in this study. The guild of species that constitutes “evergreen cover” matters greatly in this context. In this study, we deliberately selected sites and plots representative of dwarf berry shrubs, two of which (*E. nigrum* and *V. vitis-idaea*) are prostrate evergreen shrubs. Our results show that *V. vitis-idaea* cover decreased significantly over time, which may be influencing growth trends for this functional group. Evergreen plant response to warming also depends heavily on soil fertility, moisture and the presence of permafrost (Hudson and Henry 2010, Elmendorf et al. 2012, Zamin et al. 2014), indicating there may have been some unaccounted for topo-edaphic gradients within our network of mesic sites.

4.4.2 Fruit production

Our results on fruit production generally align with our predictions that berry shrubs with height plasticity are less affected by experimental warming and upright deciduous shrub growth than their prostrate berry shrub neighbours. In fact, we identified mainly positive predictors of *V. uliginosum* fruit presence, including ‘Time’ and *V. uliginosum* growth traits (cover and height). This result suggests that *V. uliginosum* may be benefitting from warming by increased flower production (Aerts et al. 2006), and/or has yet to reach a growth-reproduction trade-off, which is widely anticipated with future warming and shrubification (Lévesque et al. 2012). If cover and height of *V. uliginosum* and *B. glandulosa* continue to increase throughout the eastern Sub-Arctic region, as demonstrated in this study (Table 4.2), canopy overlapping, and crowding will likely increase the importance of interspecific competition (Kudo and Suzuki 2003), with the potential to drive growth-reproduction trade-offs among neighbours.

Collectively, fruit production in prostrate berry shrubs responded negatively to treatment effects in this study. However, our two-part conditional hurdle models revealed that the mechanisms driving changes in fruit production may be different between *E. nigrum* and *V. vitis-idaea*. For *E. nigrum*, *B. glandulosa* height (> 15-20 cm) and warming had a negative effect on the occurrence of fruit, indicating constraints on reproductive effort (flower production). Canopy constraints on reproductive effort of *E. nigrum* have been attributed to light limitation among other factors in boreal (Zvereva and Kozlov 2004), treeline (Lussier 2016) and tundra (Pajunen et al. 2011) ecosystems.

However, this interaction can shift from competition to facilitation in stressful and/or disturbed habitats (Zvereva and Kozlov 2004). The amount of *E. nigrum* fruit also decreased with time and experimental warming, indicating additional constraints on reproductive success. *Empetrum nigrum* thrives in nutrient-poor environments, and its largely intolerant of light and moisture stress (Bell and Tallis 1973). Therefore, near-ground warming could be increasing soil productivity, reducing moisture and light availability, leading to increased interspecific competition (Kudo and Suzuki 2003).

For *V. vitis-idaea*, we observed a higher likelihood of fruit over time and among warming plots, yet the amount of fruit declined over time and with warming of this species. We also observed a positive effect of *B. glandulosa* height (up to 20 cm) on the amount of *V. vitis-idaea* fruit, suggesting *B. glandulosa* may be ameliorating or nursing fruit development in *V. vitis-idaea.* Collectively, these results suggest greater constraints on reproductive success (pollination and fruit development), rather than reproductive effort (flower production) in this species. Also, *V. vitis-idaea* was the only species to exhibit a negative time-warming interaction on fruit presence, suggesting there may be increasing climatic constraints on flower development in this species. Although *V. vitis-idaea* can perform better among companion species like *E. nigrum* (Shevtsova et al. 1997), growth and fruit production of *V. vitis-idaea* in Sub-Arctic ecosystems is limited by interspecific competition (Shevtsova et al. 1995). Having very limited height plasticity, differences in winter and the following spring conditions will likely play an important role in predicting annual variation in *V. vitis-idaea* fruit production, since later snowmelt timing and longer duration of snow cover directly improve reproductive performance of this species (Krab et al. 2018).

For *V. uliginosum* and *E. nigrum*, climate variables helped to explain some variation in the occurrence of fruit, however the effect is ambiguous and could be due to location effects and potentially imprecise tracking of local climate.

The positive predictive power of individual berry species' growth traits (mainly cover) on fruit production (reproductive effort and success; Table 4.3) reinforces the importance of abundance/cover as a coarse proxy metric for fruit production (Lashley et al. 2014). As long-lived, predominantly clonal species, greater abundance/cover of dwarf berry species ensures persistence across the tundra landscape by increasing pollinator attraction, pollination success, and seed dispersal via tundra frugivores. If *B. glandulosa* continues to reduce cover of neighbouring dwarf tundra species across the eastern Low and Sub-Arctic (Ropars et al. 2015b), we can anticipate impacts throughout the pollinator network (Kettenbach et al. 2017), which could have large-scale impacts on dwarf berry shrub fruit production. As we continue to track the movement of tall shrub tundra ecosystems across treeline and tundra, it is possible that remote sensing of dwarf shrub tundra cover could be used as a surrogate to predict changes in tundra fruit availability across the landscape.

4.4.3 Other considerations and next steps

Biotic interactions, especially in the form of ungulate herbivory, have the potential to mediate climate-induced shrub expansion throughout the tundra biome (Olofsson et al. 2009, Christie et al. 2015). However, in eastern Low and Sub-Arctic Canada, migratory caribou populations such as the George River herd are rapidly declining (Côté et al. 2012), suggesting that caribou grazing is not an important constraint on growth or reproductive trait responses throughout this study. That said, our estimates of growth traits and fruit production were undoubtedly affected by other tundra herbivores and frugivores (Barrio et al. 2016), including black (*Ursus americanus* Pallas) and polar bears (*U. maratimus* Phipps.), lemmings (*Dicrostonyx hudsonius* Pallas) and other tundra rodents, arctic hare (*Lepus arcticus* Ross), insects and birds such as partridge (*Lagopus* spp.) and Canada geese (*Branta canadensis* L.). Collectively, herbivory could be contributing to high plot and site level variation in plant performance throughout this study.

Although we have identified that experimental warming constrains fruit production of prostrate berry species in the short-term, longer-term monitoring is required to track species-specific responses through time. This is especially relevant for *V. uliginosum*, which was resilient to warming and *B. glandulosa* height throughout this study. Plot-level monitoring of topo-edaphic characteristics is also required to tease apart the local mechanisms driving divergent responses in growth and reproductive traits among dwarf berry species. Future monitoring should track upright deciduous-dwarf berry shrub interactions across tundra ecotonal boundaries to better estimate anticipated feedbacks into broader tundra ecosystem function.

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Table 4.1 Locations and characteristics of experimental warming sites included in this study[1].

Inuit Region	Latitude/ Longitude	Bioclimatic Zone[1]	Vegetation Type[1]	Permafrost Type[2]	Decadal climate summaries (2000-2009)[3]				
Location (Year established)					Mean total annual precipitation (mm)	Mean annual/max./min. temperature (°C)			Degree days > 5° C
Nunavik									
Kangiqsualujjuaq (2 sites; 2008)	58.71 N 65.99 W	Eastern Sub-Arctic	Forest-tundra	C/D	697.4*	-3.6	-1.4*	-9.6*	684.1
Kangiqsujuaq (2008)	61.59 N 71.95 W	Eastern Low Arctic	Forest tundra, erect/dwarf-shrub tundra	C	449.4*	-5.7	-4.6*	-11.4*	369.4
Nunatsiavut									
Nain (2009)	56.54 N 61.69 W	Eastern Sub-Arctic	Forest-tundra	D	882.5	-1.8	2.4	-6.0	578.6
Torr Bay (2009)	58.46 N 62.82 W	Eastern Sub-Arctic	Erect/dwarf-shrub tundra	D	791.11*	-5.0*	-0.9*	-9.2*	318.3

[1] Bioclimatic zone, vegetation type and permafrost interpreted from Circumpolar Arctic Vegetation Map (CAVM Team 2003); [2] C = Continuous, D = Discontinuous; [3] Canadian Climate Normals (http://climate.weather.gc.ca/climate_normals/index_e.html) were only available for Nain, therefore we calculated a decadal climate summary based on the most recent decadal data available for all locations (2000-2009). Where possible, climate summaries were derived from local station data available through Environment Canada's historical data archive (http://climate.weather.gc.ca/historical_data/search_historic_data_e.html); data accessed Feb, 2014.; When local data

were absent (*), summaries were based on gridded monthly mean high resolution (0.5 x 0.5 degree) climate data available from the Climatic Research Unit, Time-Series 3.1 (CRU TS3.1), University of East Anglia CRU, 2011.

Table 4.2 Summary of vegetation community response to short-term experimental warming based on random intercept only linear mixed-effect models. Global response parameters included: lifeform cover (%) for all major functional groups, upright shrub (Begl = *Betula glandulosa*) and berry shrub (Emni = *Empetrum nigrum*; Vaul = *Vaccinium uliginosum*; Vavi = *V. vitis-idaea*) cover (%) and height (cm). Random factors included 'Site' and nested 'Plot ID'; Fixed factors included 'Treatment' (OTC vs. CTL), 'Time' (2008/2009 vs. 2011), and 'Treatment'*'Time'. Models were specified using unstandardized, zero truncated data (Gaussian/gamma error family and identity/log link) and coefficients retained at $p < 0.1$.

	Random factors		**Fixed factors**			**Model performance**	
Community response	**Site**	**Plot ID**	**Treatment (CTL vs OTC)**	**Time**	**Treatment x Time**	**Log likelihood**	**ΔAIC**
Lifeform Cover (%)							
Shrubs (all)	X	X	–	–	–	-1234.35	4.9
Deciduous	X	X	–	↑	–	-1010.92	3.5
Evergreen	X	X	–	↓ *	–	-1246.74	3.1
Forbs	X	–	–	↑	–	- 594.32	3.0
Graminoids	–	X	–	↓	–	- 616.03	3.4
Lichens	X	X	–	–	–	-1031.28	4.7
Mosses	X	X	–	↓	–	- 732.31	1.4
Upright shrub							
Begl Cover (%)	X	X	–	↑	–	- 741.53	0.9
Begl Height (cm)	X	X	X	X	↑	- 537.97	11.6**
Berry shrub							
Vaul Cover (%)	X	X	–	↑	–	-897.67	3.3
Vaul Height (cm)	X	X	–	↑	–	-487.23	2.7
Emni Cover (%)	X	X	–	–	–	-691.80	4.9
Emni Height (cm)	X	X	–	↑	–	-278.23	3.9
Vavi Cover (%)	X	X	–	↓	–	-927.71	3.7
Vavi Height (cm)	X	X	–	↑	–	-474.67	2.8

***** X denotes when a term was retained in the model; ↑ and ↓ indicate significant direction of change across fixed factors at *p* <0.05; '******' indicates significance at *p* <0.1; '–' indicates insignificant factors removed during model selection; 'CTL' = control and 'OTC' = open-top warming chamber; ΔAIC indicates AIC_{global} - AIC_{min}; NA when indicates AIC_{global} = AIC_{min}

Table 4.3 Fitted hurdle model summary for the effects of short-term experimental warming, vegetation community attributes and local climate on fruit production of a) *Vaccinium uliginosum* (Vaul), b) *Empetrum nigrum* (Emni) and c) *V. vitis-idaea* (Vavi) based on random intercept only mixed-effects hurdle models. Random factors included ‘Site’ and nested ‘Plot ID’; Fixed factors included ‘Treatment’ (OTC vs. CTL), ‘Time’ (2008/2009 vs. 2011), and ‘Treatment’*’Time’; Fixed effects included cover and height of each focal berry species and *Betula glandulosa* (Begl), and local climate variables (JJA/DJF air temperature). Step 1 models the probability of fruit production (presence/absence fruit/m^2; binomial error, logit link), and Step 2 the extent of fruit production (total # fruit/m^2; negative-binomial error, log link). Model statistics were derived from unstandardized data; Coefficients were retained at *p* <0.10 (bold). OTC = open-top warming chamber; CTL = control; JJA = June, July August, and DJF = December, January, February. Δ AIC represents the difference in Akaike Information Criteria (AIC) between the best-fit model and the global model.

Berry Shrub	Hurdle	Effects	Coefficients/ Intercepts	Estimate/ Variance*	Std. Error/ Std.Dev*	Z-Value	P-Value	ΔAIC	Log Likelihood
a. Vaul	**Step 1**	Random	Plot ID	2.01	1.42			1.6	-125.30
		Fixed	Intercept	-0.58	0.95	-0.61	0.541		
			Vaul cover (%)	0.09	0.02	3.86	**<0.001**		
			Vaul height (cm)	0.22	0.08	2.67	**0.007**		
			JJA Temp (°C)	-0.31	0.11	-2.68	**0.007**		
			Time	1.36	0.44	3.06	**0.002**		
	Step 2	Random	Site	0.31	0.55			9.6	-796.3
			Plot ID	0.27	0.51				
		Fixed	Intercept	3.72	0.35	10.46	**<0.001**		
			Vaul cover (%)	0.03	0.01	3.87	**<0.001**		
b. Emni	**Step 1**	Random						5.9	NA
		Fixed	Intercept	0.25	1.62	0.15	0.875		

			Emni cover (%)	0.13	0.02	5.62	**<0.001**		
			Emni height (cm)	0.32	0.09	3.33	**<0.001**		
			Begl height (cm)	-0.10	0.05	-2.16	**0.030**		
			JJA Temp. (°C)	0.21	0.10	2.04	**0.041**		
			DJF Temp. (°C)	0.26	0.11	2.37	**0.020**		
			Treatment (OTC)	-0.77	0.41	-1.85	**0.064**		
	Step 2	Random	Plot ID	0.11	0.33			9.4	-671.2
		Fixed	Intercept	4.89	0.24	20.07	**<0.001**		
			Emni cover (%)	0.03	0.00	5.20	**<0.001**		
			Treatment (OTC)	-0.43	0.22	-1.96	**0.050**		
			Time	-0.90	0.22	-4.10	**<0.001**		
c. Vavi	**Step 1**	Random	Site	6.64	2.57			9.9	-126.90
			Plot ID	1.49	1.22				
		Fixed	Intercept	-1.84	1.37	-1.34	0.178		
			Vavi cover (%)	0.12	0.03	3.92	**<0.001**		
			Time	2.71	0.70	3.84	**<0.001**		
			Treatment (OTC)	0.29	0.60	0.49	0.622		
			Treatment*Time	-1.37	0.77	-1.74	**0.076**		
	Step 2	Random	Site	0.92	0.96			1.2*	-760.3
			Plot ID	0.26	0.51				
		Fixed	Intercept	3.72	0.54	6.84	**<0.001**		
			Vavi cover (%)	0.06	0.01	4.60	**<0.001**		
			Begl height (cm)	0.05	0.02	2.87	**0.004**		
			Treatment (OTC)	-0.35	0.20	-1.76	**0.080**		
			Time	-0.77	0.20	-3.74	**<0.001**		

*ΔAIC after collinear interaction terms were removed from global model

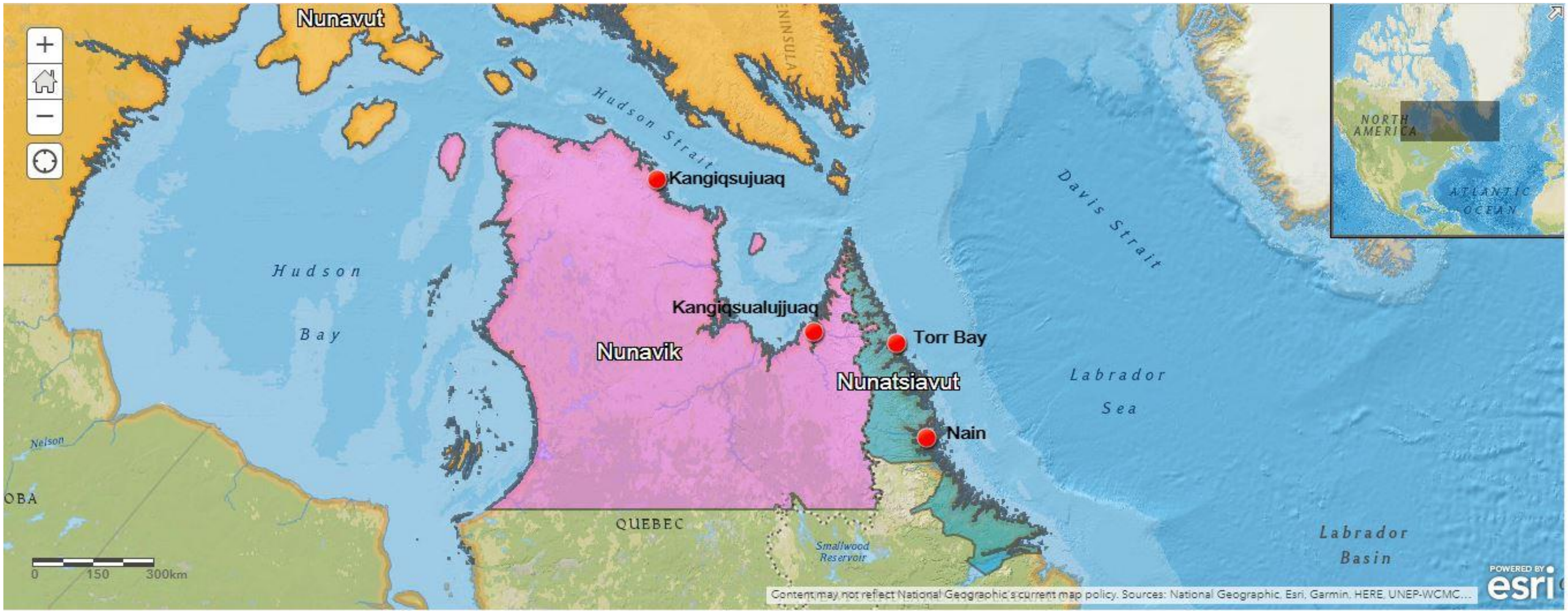

Fig. 4.1 Map of experimental warming studies established in 2008 (Kangiqsujuaq and Kangiqsualujjuaq, Nunavik) and 2009 (Torr Bay and Nain, Nunatsiavut). Map depicts regional (Inuit Regions of Canada) and vegetation boundaries between the boreal/taiga (green) and tundra (grey) zones (Map prepared through ArcGIS - ESRI online, 2018).

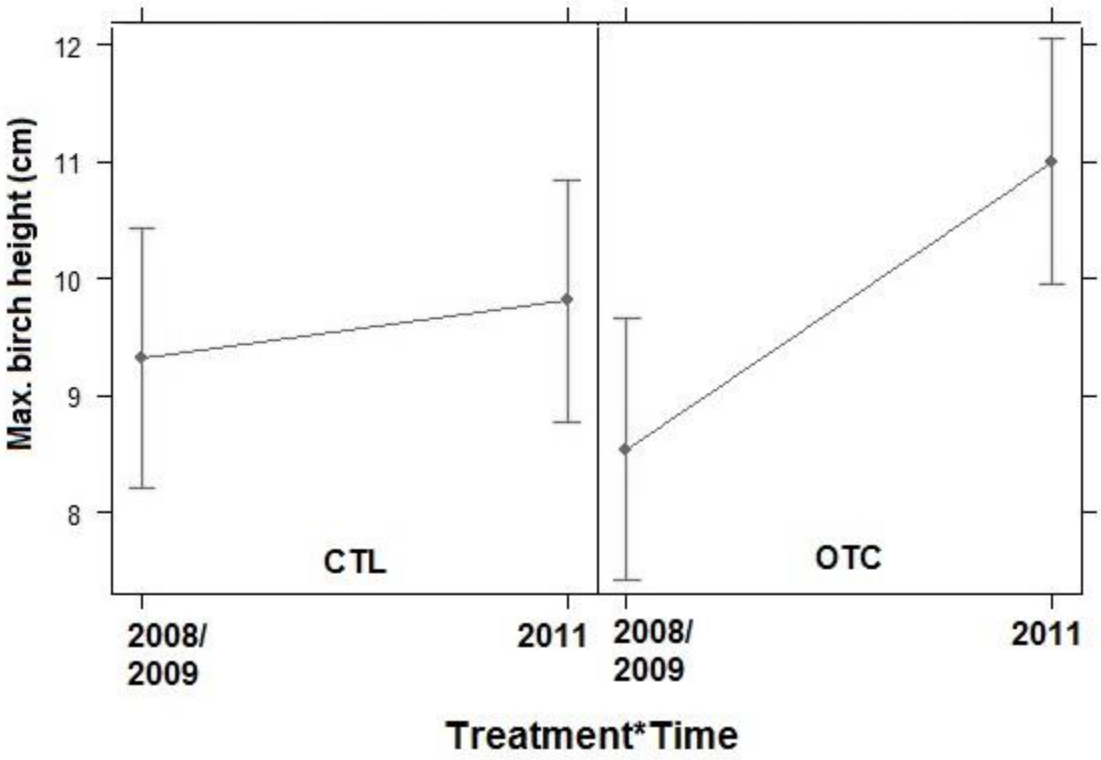

Fig. 4.2 Fixed effect plot indicating the magnitude and strength of interaction effects (Treatment*Time) on ‘Maximum birch height’ (cm), as determined by random intercept only linear mixed-effect models summarized in Table 4.2. Error bars = standard error; CTL = control and OTC = open-top warming chamber.

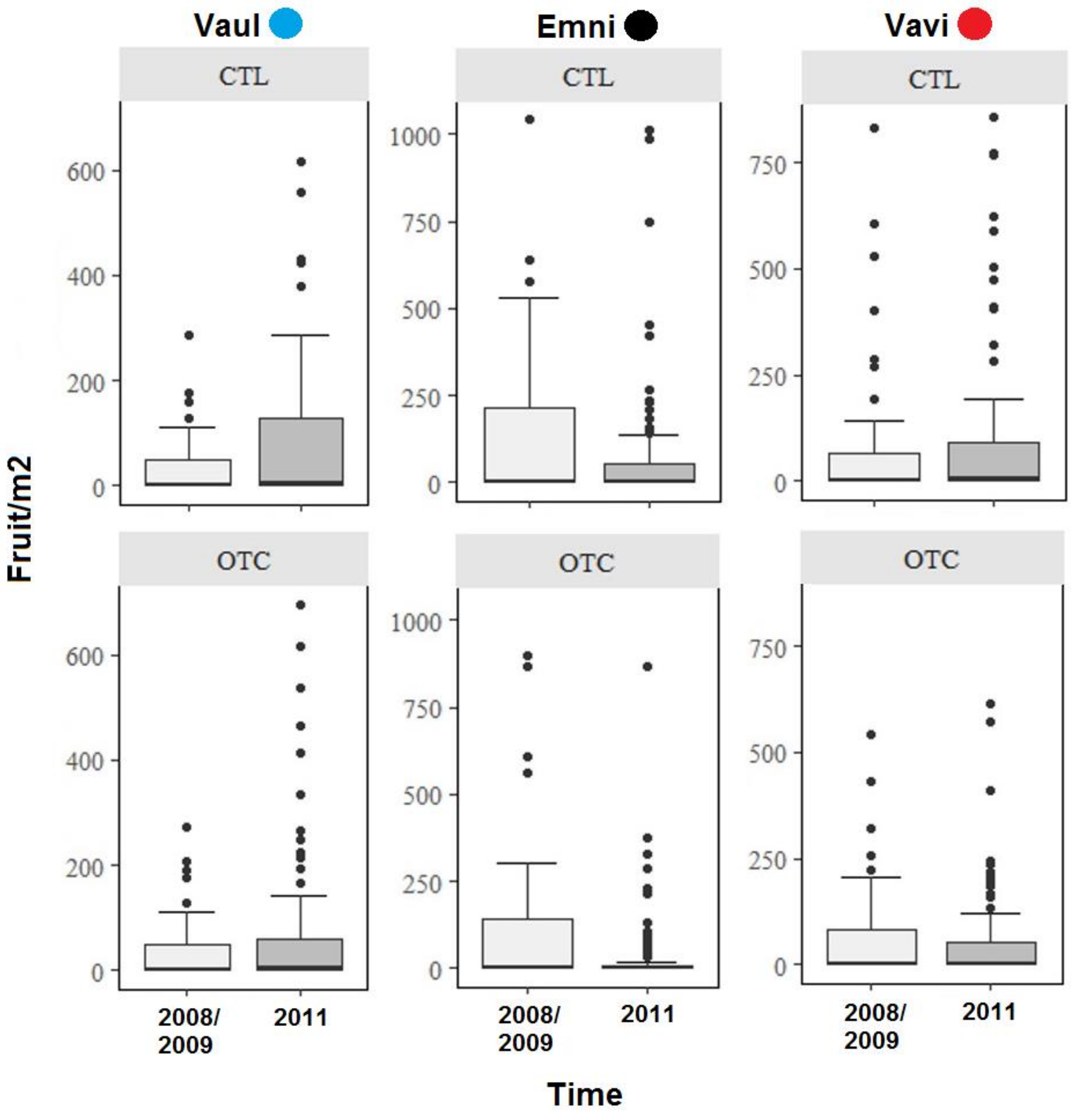

Fig. 4.3 Boxplots showing fruit production (total # fruit/m^2) (median, interquartile range, min/max and outliers) of *Vaccinium uliginosum* (Vaul), *Empetrum nigrum* (Emni) and *V. vitis-idaea* (Vavi) between controls (CTL) and open-top warming chambers (OTC) across five sites over time. Nunavik sites (Kangiksualujjuaq-1,2 and Kangiqsujuaq) were established in 2008 and Nunatsiavut (Nain and Torr Bay) in 2009.

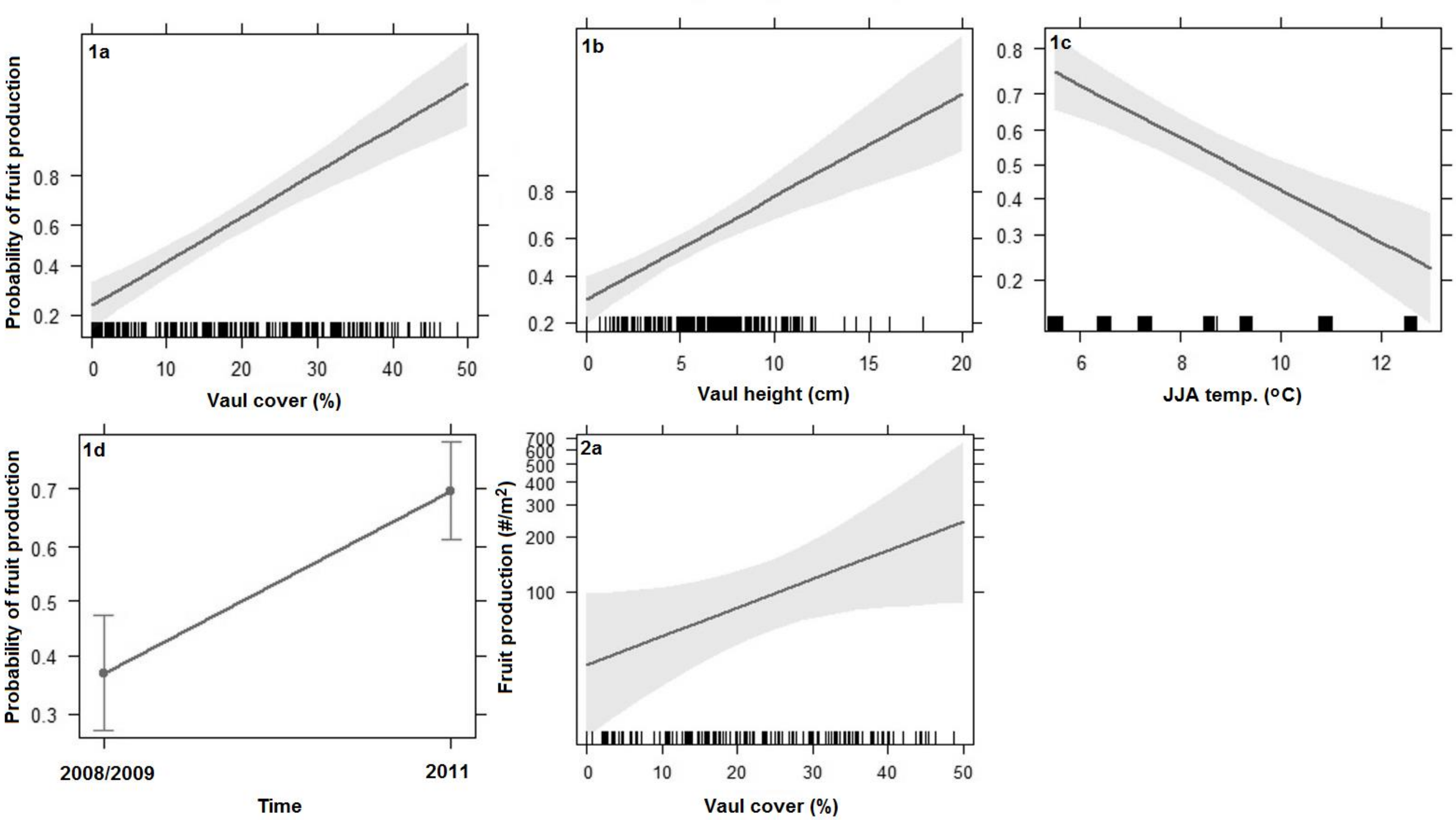

Fig. 4.4 Fixed effect plots indicating the magnitude and strength of significant parameter effects on the probability (1a-d) and extent (2a) of fruit production in *Vaccinium uliginosum* (Vaul), as determined by generalized linear mixed-effects hurdle models summarized in Table 4.3. Shaded areas represent 95% confidence intervals; Error bars = standard error; CTL = control and OTC = open-top warming chamber; JJA = June, July, August; Black lines along x-axis represent predictor observations and their raw values.

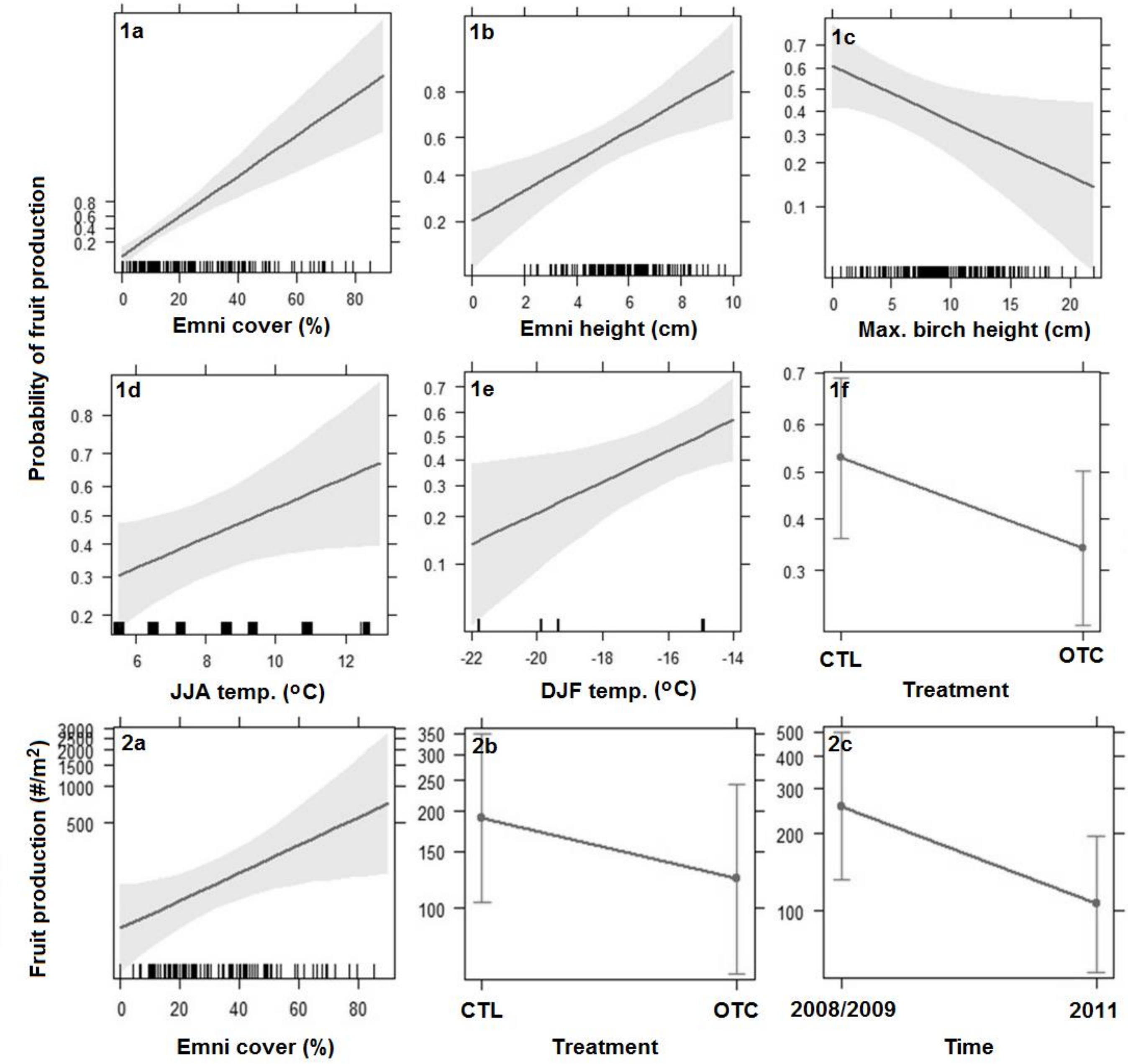

Fig. 4.5 Fixed effect plots indicating the magnitude and strength of significant parameter effects on the probability (1a-f) and extent (2a-c) of fruit production in *Empetrum nigrum* (Emni), as determined by generalized linear mixed-effects hurdle models summarized in Table 4.3. Shaded areas represent 95% confidence intervals; Error bars = standard error; CTL = control and OTC = open-top warming

chamber; JJA = June, July and August; DJF = December, January and February; Black lines along x-axis represent predictor observations and their raw values.

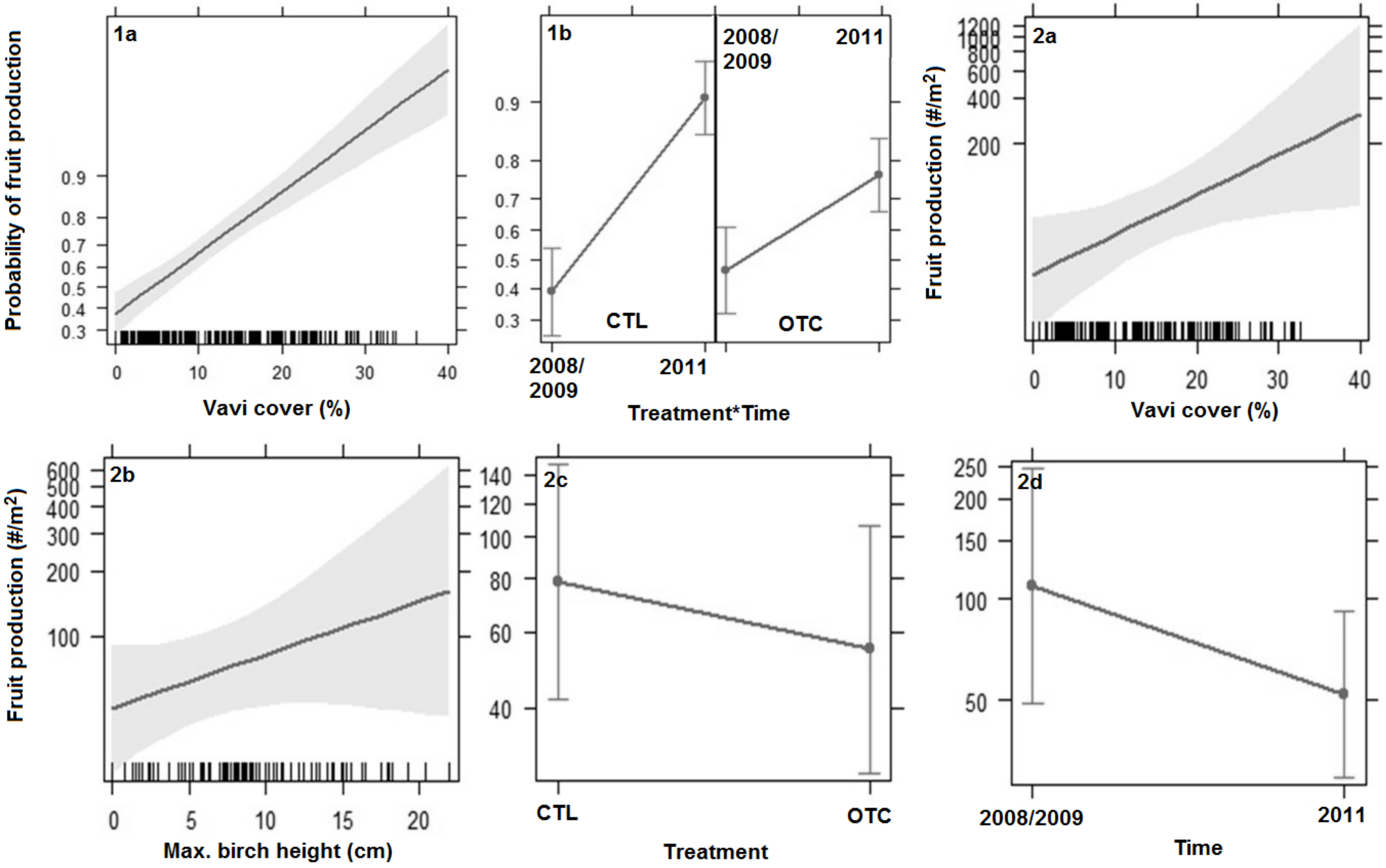
1a
Probability of fruit production
0.3
0.4
0.5
0.6
0.7
0.8
0.9
0
10
20
30
40
Vavi cover (%)
1b
CTL
OTC
2008/
2009
2011
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Treatment*Time
2a
Fruit production (#/m^2)
200
400
600
800
1000
1200
0
10
20
30
40
Vavi cover (%)
2b
Fruit production (#/m^2)
100
200
300
400
500
600
0
5
10
15
20
Max. birch height (cm)
2c
40
60
80
100
120
140
CTL
OTC
Treatment
2d
50
100
150
200
250
2008/2009
2011
Time

Fig. 4.6 Fixed effect plots indicating the magnitude and strength of significant parameter effects on the probability (1a-b) and extent (2a-d) of fruit production in *Vaccinium vitis-idaea* (Vavi), as determined by generalized linear mixed-effects hurdle models summarized in Table 4.3. Shaded areas represent 95% confidence intervals; Error bars = standard error; CTL = control and OTC = open-top warming chamber; Black lines along x-axis represent predictor observations and their raw values.

Appendix 4.1 Summary of experimental warming set-up and sample methodologies across four locations and five sites in this study.

Inuit Region Location	Sample size (OTC/CTL pairs)	Year established Year resampled	Survey method	Plot size (cm)	Sample intensity (# grid points)	Fruit harvest area (cm)
Nunavik						
Kangiqsualujjuaq	N=14 (Site 1) N=12 (Site 2)	2008	Point frame	70 x 70	50	25 x 25 (Site 2 =ND*)
		2011	Point frame	70 x 70	100	70 x 70
Kangiqsujuaq	N=12	2008	Point frame	70 x 70	50	25 x 25
		2011	Point frame	70 x 70	50	70 x 70
Nunatsiavut						
Nain	N=9	2009	Point frame	70 x 70	49	ND*
		2011	Point frame	70 x 70	49	70 x 70
Torr Bay	N=30	2009	Point frame	70 x 70	49	35 x 35
		2011	Point frame	70 x 70	49	70 x 70

*ND = no data.

Appendix 4.2 Pearson product moment p-values (adjusted Holm's method) indicating significant correlations between seasonal temperature and degree day predictor variables at *p* <0.05*.

	DJFTemp	FDD	GDD	JJATemp	TDD	xATemp	xSumTemp	xWintTemp
DJFTemp	1	**<.0001**	**<.0001**	<.0001	**<.0001**	<.0001	0.0002	<.0001
FDD	**<.0001**	1	0.7491	1	0.2051	<.0001	**0.0014**	**<.0001**
GDD	**<.0001**	0.7491	1	**<.0001**	<.0001	<.0001	**<.0001**	0.9942
JJATemp	**<.0001**	1	**<.0001**	1	**<.0001**	<.0001	<.0001	1
TDD	**<.0001**	0.2051	<.0001	**<.0001**	1	<.0001	**<.0001**	0.3893
xATemp	**<.0001**	**<.0001**	**<.0001**	<.0001	**<.0001**	1	<.0001	<.0001
xSumTemp	0.0002	**0.0014**	**<.0001**	<.0001	**<.0001**	<.0001	1	0.0076
xWintTemp	<.0001	**<.0001**	0.9942	1	0.3893	<.0001	0.0076	1

*DJF = December, January, February; JJA = June, July, August; FDD/GDD/TDD = Freezing, Growing and Thawing degree days; xA = Mean annual; xATemp = Mean annual temperature; xSumTemp = Mean summer temperature, xWintTemp = Mean winter temperature.

Appendix 4.3 R-code for generalized linear mixed hurdle models using packages ‘MASS’ (Venables and Ripley 2002), lme4 (Bates et al. 2015), glmmADMB (Bolker et al. 2013), and ‘effects’ (Fox 2003).

Hurdle Step 1:

```
>library(lme4)
>ModelName<glmer(Y~(1|Site/PlotID) + X1 +Xx +…..Xz + (X1*Xx), na.action=na.omit,
data = , family="binomial")
```

Hurdle Step 2:

```
>library(glmmADMB)
>ModelName<glmmadmb(Y~(1|Site/PlotID)+ X1 +Xx +…..Xz + (X1*Xx), family="nbinom",
data = subset(, Y > 0))
```

Effects Displays:

```
>library(effects)
> plot(allEffects(model),rescale.axis=FALSE)
```

Chapter 5: Fruit production decreases among culturally important prostrate berry shrubs following seven years of experimental warming in Sub-Arctic Labrador, Canada

Siegwart Collier, L., L. Hermanutz, A. Cuerrier

Abstract

Understanding how climate variability and warming contributes to recently observed changes in berry resources is necessary to mitigate negative impacts on Indigenous subsistence practices and cultural systems, and to determine broader feedbacks into tundra ecosystem processes and food webs. In this study, we focus on the role of local topo-edaphic conditions and shrubification as important drivers of change in tundra berry resources in the Nunatsiavut region of eastern Sub-Arctic Canada. Eastern Sub-Arctic Canada is experiencing pronounced recent warming (Brown et al. 2012, Candlish et al. 2015, Ju and Masek 2016, Bush and Lemmen 2019) with well-documented positive influences on height, abundance and distribution of upright deciduous shrubs (Fraser et al. 2011, Ropars and Boudreau 2012, Tremblay et al. 2012). These changes are consistent with Inuit knowledge and observations of changes in plant and berry resources. We examined the relationship between dwarf birch (*Betula glandulosa* Michx) and three culturally important dwarf berry shrubs [*Empetrum nigrum* L. (black crowberry), *Vaccinium vitis-idaea* L. (mountain cranberry/lingonberry) and *Vaccinium uliginosum* L. (alpine blueberry)] after seven years of experimental warming (2009 to 2016) to determine the potential impacts on plant community attributes and fruit production. All focal berry species grew taller over time within experimental warming plots; however, *Vaccinium* spp. also became less abundant, suggesting a phenotypic response to changing resource availability. Changes in the occurrence and abundance of fruit were species-specific, but we detected a gradient in response to experimental warming whereby fruit production in truly prostrate berry shrubs, *V. vitis-idaea* and *E. nigrum*, was more sensitive to experimental warming than *V. uliginosum*, which is capable of upright growth. Inclusion of local topo-edaphic variables from 2011 to 2016 enabled us to identify that conditions are becoming warmer and drier in our warming experiments; however, effects of these changes on fruit production were marginal. *Vaccinium vitis-idaea* was the only species to demonstrate a negative response in fruit occurrence and abundance with increasing *B. glandulosa* abundance, suggesting that fruit production in *V. vitis-idaea* is most vulnerable to tundra shrubification.

Keywords: Fruit production, dwarf berry shrubs, shrub expansion, eastern Sub-Arctic Canada, Nunatsiavut Labrador, experimental warming, *Vaccinium uliginosum*, *Vaccinium vitis-idaea*, *Empetrum nigrum*, *Betula glandulosa*

5.1 Introduction

The tundra biome is rapidly changing due to contemporary climate variability and warming (Post et al. 2009, IPCC 2014). Across Inuit Nunangat and Sub-Arctic Indigenous regions in Canada, the impacts of climate change are already being experienced across a variety of socio-economic and food systems (Downing and Cuerrier 2011, Ford et al. 2015, Gerin-Lajoie et al. 2016). Within plant-food systems, Indigenous knowledge holders have identified important changes in berry resources linked to climate warming and variability, including both decreases and increases in berry growth, quantity, quality, ripening times, access and availability (Chapter 2, Cuerrier et al. 2015, Gerin-Lajoie et al. 2016, Anderson et al. 2018, Boulanger-Lapointe et al. 2019a). Berries are a staple food within Inuit diets (Zutter 2009, Clarke 2012, Boulanger-Lapointe et al. 2019a). Harvesting, preparation and consumption of berries contributes to maintaining cultural heritage, while supporting community health and well-being (Cunsolo Willox et al. 2012). Dwarf berry shrubs also play an important role in tundra ecosystem structure and function by providing forage (Richardson et al. 2002, Cadieux et al. 2005, Christie et al. 2015) and habitat (Marcot et al. 2015) for vertebrate and invertebrate herbivores, supplying nutrients and storing carbon in above-/belowground biomass and litter (Shaver et al. 1992, Grafius and Malanson 2015), and by mediating local climate through impacts on snow abundance and distribution (Myers-Smith et al. 2011), and permafrost freeze-thaw cycles (Blok et al. 2010). Understanding how climate variability and warming contributes to recent changes in berry resources is necessary to mitigate negative impacts on Indigenous subsistence practices and cultural systems, and to determine broader feedbacks into tundra ecosystem processes.

Wild berries are a naturally variable resource that is challenging to predict due to a complex interplay of exogenous and endogenous factors contributing to flower and fruit production (Krebs et al. 2009). In the context of climate change and tundra berry shrub performance, mechanisms of climate-driven changes fall into two broad categories: 1) changes in climate variables (extreme and gradual) that influence plant phenology (timing of leaf out, shoot elongation, bud development, flowering and ripening, and flower production), and 2) ecological factors, abiotic and biotic, that influence plant growth and distribution (Parmesan and Hanley 2015). Monitoring and manipulation of winter climate variables (i.e. precipitation and temperature) has shown that changes in snow depth and snowmelt timing (Wipf et al. 2009, Wipf 2010), and the occurrence of extreme winter warming, thawing and icing events (Bokhorst et al. 2009, Bokhorst et al. 2012, Preece et al. 2012, Preece and Phoenix 2014) can profoundly affect plant phenology, with species-specific consequence on fruit production. Ecological research throughout the forest-tundra ecotone points to climate-driven tall-shrub expansion (aka shrubification) (Myers-Smith et al. 2011, Ropars et al. 2015b), changing snow and permfrost distribution (Myers-Smith et al. 2015, Anderson et al. 2018), and herbivory (Barrio et al. 2016, Boulanger-Lapointe et al. 2017) as important ecological mechanism of change in berry resources. Climate-driven changes in fruit production are most likely a combination of direct (climatic) and indirect (ecological) factors, but community-based evidence stresses that local factors, such as topo-edaphic variation, play a critical role in predicting changes in berry resources (Boulanger-Lapointe 2017, Rapinski et al. 2017).

Climate-driven expansion (upright and spatial) of tall shrubs has the potential to influence climate and resource availability across several spatial scales (Vowles and Björk 2019). Locally, taller and denser patches of deciduous shrubs can increase understory shading (Juszak et al. 2014), and alter soil moisture and temperature through the insulative effect of snow trapping (Sturm et al. 2005), which in turn causes increased soil nutrient (N) mineralization and decomposition rates (DeMarco et al. 2014). How tundra berry species respond in terms of growth, flower and fruit production will depend on their life history strategies. For example, although lessening the climatic constraints on soil physical properties is generally beneficial to tundra plant growth, conditions of lower light tend to shift resource allocation away from sexual reproduction (such as flower production) in favour of asexual reproduction in the form of vertical/lateral growth and increased leaf area (Yang and Kim 2016). Less investment in flower production can decrease pollination success and therefore fruit production for shrub species, since fewer flowers will be less effective in attracting visitation from pollinators (Scaven and Rafferty 2013).

In this study, we focus on the role of local topo-edaphic conditions and shrubification as important drivers of change in tundra berry resources in the Nunatsiavut region of eastern Sub-Arctic Canada. Eastern Sub-Arctic Canada, which includes the Inuit regions of Nunavik and Nunatsiavut, is experiencing pronounced recent warming (Brown et al. 2012, Candlish et al. 2015, Bush and Lemmen 2019) with well-documented positive influences on height, abundance and distribution of upright deciduous shrubs (Fraser et al. 2011, Ropars and Boudreau 2012, Tremblay et al. 2012), and Inuit knowledge of changes in plant and berry resources (Cuerrier et al.

2015, Gerin-Lajoie et al. 2016, Boulanger-Lapointe et al. 2019a). Within this context, proximity to the Labrador Sea and mountainous topography create a unique coastal mountain climate across Nunatsiavut, which is characterized by abundant precipitation, cold summer air temperatures, and the prevalence of coastal summer fog (Brown et al. 2012). In Nunatsiavut, air temperatures have increased by almost 2°C since the 1990's (Brown et al. 2012, Way and Viau 2015). Projected changes over Nunatsiavut for the 2041-2070 period indicate average air temperature increases of 2-4°C, increased daily temperatures in fall and winter months, lengthening of the growing season and growing degree days, a shortening of the snow and ice-cover season, as well as more precipitation in the form of rain (Brown et al. 2012, Finnis and Daraio 2018). If realized, predicted conditions will inevitably alter local climate, and would continue to support treeline and tundra shrubification, suggesting strong potential for accelerated effects on Nunatsiavut berry resources. Identifying which berry species are most susceptible to climate impacts will be important to distinguish for local and regional land-use planning.

Here, we present a multi-species, multi-year analysis on the relationship between the expanding tall shrub *Betula glandulosa* Michx. (arctic dwarf birch, AvâlaKiak) and three culturally significant dwarf berry shrubs [*Vaccinium uliginosum* L. (northern bilberry, alpine blueberry, kigutanginnak), *Empetrum nigrum* (blackberry, black crowberry, Paungak), and *Vaccinium vitis-idaea* L. (redberry, mountain cranberry, lingonberry, kimminak)] under experimental warming conditions in Nunatsiavut, Labrador, Canada. These berry species are ubiquitous throughout the forest-tundra ecotone in Nunatsiavut, and they share many life history traits characteristic of clonal dwarf shrubs. However, focal shrubs differ greatly in their ability to accrue height based on their mode and capacity for stem growth (Chapters 3 and 4). Among the prostrate berry shrubs, *V. uliginosum* exhibits the greatest phenotypic plasticity in maximum height (70-100 cm) (Jacquemart 1996), followed by *E. nigrum* (50 cm) (Bell and Tallis 1973) and *V. vitis-idaea* (30cm) (Ritchie 1955). In contrast, *B. glandulosa* is an upright canopy-forming deciduous shrub with significant growth plasticity. In its prostrate form, erect stems range from 10-40 cm (Aiken et al. 2003), yet in elevational areas it can reach up to 2.5 m in height (Hermanutz et al. 1989). Based on the differences in their growth plasticity, we predict that:

1) Experimental warming will have positive effects on growth (cover and height) of *B. glandulosa* and other upright deciduous and tall shrubs, and negative effects on growth of ground dwelling vegetation. Dwarf berry shrubs, having varying life history strategies and growth plasticity, will respond along a gradient, with more positive effects on cover and height of *V. uliginosum* followed by *E. nigrum* and *V. vitis-idaea* respectively. These changes will coincide with a shift in near ground microclimate towards less available light, on average warmer soil temperatures and less soil moisture in experimental warming plots versus control plots.
2) Experimental warming and upright deciduous shrub growth (cover and height) will have negative effects on fruit production of dwarf berry shrubs. Fruit production in prostrate berry shrubs (*V. vitis-idaea* and *E. nigrum)* will be more negatively affected than fruit production in *V. uliginosum* given the latter species' plasticity in upright growth. Available light will constrain fruit production in

prostrate berry shrubs (*V. vitis-idaea* and *E. nigrum)* between experimental warming plots and controls.

5.2 Methods

5.2.1 Study Sites

Study sites were established in 2009 in Nain (56°33 N, 61°41 W) and Torr Bay (58°46 N 62°82 W) Nunatsiavut (northern Labrador), Canada (Fig. 5.1), which are coastal sites representative of the Eastern Sub-Arctic Tundra Bioclimatic Subzone (CAVM Team 2003). Vegetation ranges from forest-tundra in Nain to erect/dwarf shrub tundra in Torr Bay (CAVM Team 2003), with the latitudinal treeline existing approximately 200km north of Nain in Napaktok Bay (Roberts et al. 2006). Sites were established in mesic, low-shrub tundra plant communities, where the shrub canopy is dominated by mainly upright deciduous species (primarily *B. glandulosa* but also *Alnus viridis* (Chaix) DC. ssp *crispa* (Aiton) Turrill [green/mountain alder] and upright *Salix* sp. L. [willow]) and in the ground layer by dwarf ericaceous shrubs (*V. uliginosum, E. nigrum* L., *V. vitis-idaea* L., *Rhododendron tomentosum* L./*R. groenlandicum* Oeder [northern/Labrador tea]). The composition of non-woody and non-vascular ground vegetation was similar between sites, however boreal species persist in Nain due to the presence of boreal forest.

Nain and Torr Bay are underlain with extensive discontinuous permafrost, which is greatly influenced by the abundance and distribution of snow throughout this region (Way and Lewkowicz 2018). Decadal climate summaries for the period of 2000-2009 show that total precipitation is similar between sites, however Torr Bay is generally cooler than Nain throughout the year, with 318.3 growing degree days above 5°C as compared to 578.6 in Nain (Table 5.1).

5.2.2 Sample Design and Data Summary

In July/August 2009, we established paired experimental warming and control plots (Nain, N=9; Torr Bay, N=30) in homogeneous mesic, low-shrub tundra following the International Tundra Experiment protocol (ITEX; http://ibis.geog.ubc.ca/itex/). Plots were resampled in 2011 and 2016 to track control and treatment effects through time. The ITEX approach creates passive tundra warming by utilizing open-top warming chambers (OTCs), which are constructed by fastening angled polycarbonate panels in a hexagonal design. These transparent panels shelter vegetation from the wind and moderate diurnal heat loss, effectively raising the mean daily summer air temperature by 1-3°C (Molau 1997). The standard ITEX plot size is 1m x 1m, and it's intended to monitor ecosystem-level change. In this study, we reduced our plot size to 70 cm x 70 cm to specifically track berry shrub performance (growth and fruit production) at the plant community level. At each plot, point-frame sampling was used to quantify species composition, abundance and height following the CANTTEX protocol (http://ipytundra.ca/sites/default/files/CiCAT%20point-framing%20protocol.pdf).

For each plot, species-level abundance was estimated as the total number of point frame hits/plot, and data were pooled by vegetation lifeforms to obtain plot-level estimates of cover for the following (broad) plant functional groups and attributes (Elmendorf et al. 2011): shrubs (all, deciduous [upright and prostrate] and evergreen), forbs, graminoids, mosses, lichens, litter and dead plant biomass. Height of all species (to the nearest 0.5 cm) was recorded at each point frame hit, and individual estimates were averaged to obtain a mean height (cm) for each species in each plot. We used *B. glandulosa* as a proxy for the upright deciduous shrub canopy layer because this species is the tallest, most dominant and frequently occurring upright deciduous shrub among sites. Given that *B. glandulosa* can exhibit significant variation in upright architecture, we used maximum rather than mean height as a response trait for the upright deciduous shrub canopy layer.

In 2011 and 2016, we quantified near-ground microclimatic conditions at the plot level by averaging three readings per plot for the following variables: ground and shrub-canopy level photosynthetic active radiation (PAR) (µmol/s/m^2; LI-COR 190 Quantum sensor and LI-250A Light meter, LI-COR, Lincoln, Nebraska, USA), soil temperature (^{0}C) and soil moisture (%) of the organic soil horizon (Delta-T W.E.T. Sensor, Hoskin Scientific, Burlington, ON). Available PAR (%) was calculated as the proportion of available PAR to reach the ground surface. Diurnal sampling variability was reduced by sampling only during overcast conditions or days with clear sky, and between 10:00am and 2:00 pm. Measures were taken over a 1-day period in Nain and 2 days in Torr Bay.

At the end of each field season when nearly all fruit had been set (mid-August), we harvested all the berries of our focal berry species within each 70 cm x 70 cm plot. Due to time constraints in 2009, berries were harvested in a subset of the plot (25 cm x 25 cm); because of this difference in harvest intensity between 2009 and subsequent years, we estimated fruit production for all years as total # fruit/species/m^2.

5.2.3 Data analysis

Community and dwarf berry shrub performance

Zero-inflation is an important characteristic among our fruit production (count) and vegetation abundance (positive continuous) datasets in this study. Although zeros are difficult to model using traditional approaches (i.e. general linear models) based on the normal error distribution (Zuur et al. 2007), they are common in ecological datasets (Warton 2005). Here, zeros represent important observations to retain because they reflect meaningful plot-level variation on the presence/absence of fruit and certain vegetation lifeforms. To better incorporate this variability, we used a two-part conditional hurdle model, which addresses the high occurrence of zeros by first estimating the probability that fruit and/or a functional group is present (Bernoulli distribution), and then if/when present, estimating the extent of fruit production and/or functional group cover using a different error distribution (fruit production = negative-binomial; functional group cover = gamma or Gaussian) (Martin et al. 2005, Zuur et al. 2012). To account for repeated measurements of the same sites and plots at multiple time-points, we used generalized linear mixed-effects models, with random intercept and fixed slopes for plots nested across our sites. This approach assumes similar baseline conditions across sites, such that our fixed effects will respond the same across our random subject groupings in the following form:

$$Y \sim (1|\text{Site/PlotID}) + X_1 + X_2 + X_x + (X_1 * X_x)$$

Where ‘Y’ = response, ‘1| Site/PlotID’ = random effect term for PlotID nested within Sites, ‘$X_{1\text{-}x}$’ = fixed effect predictors variables, and ‘$(X_1 * X_x)$’ = fixed effect interaction terms.

Mixed-effect hurdle models were applied for two purposes in this study. First, global models with random effects (‘Site’, ‘PlotID’), fixed factors (‘Treatment’, ‘Year) and fixed factor interactions (‘Treatment’ x ‘Year’) were constructed to evaluate changes in plant functional group cover, focal species’ growth traits and microclimatic variables independently. Functional groups included shrubs (all), deciduous (upright and prostrate) and evergreen shrubs, forbs, graminoids, mosses, lichens, litter and dead plant biomass. Growth traits included cover and height of *B. glandulosa* and our three focal berry species. Secondly, mixed-effect hurdle models were constructed to predict changes in fruit production. Because microclimatic data were not available for the initial sample year (2009), we ran two sets of fruit production models, with (2011-2016) and without (2009-2016) the inclusion of microclimatic data. Global fruit production models included: random, fixed factors, and fixed-factor interactions (as described above), fixed-effect terms for understory structure (‘berry species cover (%) and height (cm)’, ‘*B. glandulosa* cover and height (cm)’), within-species height-cover interactions, and microclimatic (‘Soil temperature (°C)’, ‘%PAR’ and ‘Soil moisture (%)’) parameters.

Prior to model selection, collinearities among predictor variables were investigated by calculating Pearson product moment correlation coefficients (*r*-values). We used a backwards selection strategy starting with a saturated mixed-effect model that included all possible random and fixed effects, and sequentially removed random and then fixed effects terms at p >0.1 until we arrived at our final model (Zuur 2009, Elmendorf et al. 2011). Model selection was conducted on standardized (scaled to z-scores) and unstandardized predictor variables. Although our decision on alpha was unchanged with/without standardization, we present standardized coefficients for count models (zeros removed), as they enabled model convergence. Interaction terms among random/fixed factors, growth traits and microclimate variables were considered during the initial stages of model specification, however we found that our sample size, particularly among count models, could not support inclusion of multiple interaction terms. Therefore, only fixed effect (i.e. 'Treatment*Year' and 'berry species cover*height') interactions were considered during model selection. Change in Akaike Information Criterion (ΔAIC) was calculated to compare global and candidate models (Burnham and Anderson 2002) and we relied on inspection of variance inflation factors, and residual vs. fitted values at each step to determine the model of best fit. All global models were specified using Type I sum of squares error structure and predictor variables were ordered as follows: random ('Site/PlotID') then fixed factors ('Treatment' and 'Year') followed by fixed factor interactions ('Treatment*Year').

All generalized linear mixed hurdle models were analyzed in R version 3.3.0 (R Core Team 2016) using packages 'MASS' (Venables and Ripley 2002), lme4 (Bates et al. 2015) and glmmADMB (Bolker et al. 2013). Effects displays were constructed using package 'effects' (Fox 2003). R-code is provided in Appendix 5.1.

5.3 Results

5.3.1. Growth traits and microclimatic variables

The abundance of all plant functional groups and community attributes changed significantly over time in this study, and we observed many important interactions between time and OTC's (Table 5.2; Appendix 5.2a). Irrespective of treatment, upright and prostrate deciduous shrubs increased in cover over time. However, interaction terms illustrate that upright deciduous shrubs (i.e. *B. glandulosa*) increased in OTC's from 2009-2016, and prostrate deciduous shrubs (i.e. *Salix herbacea* L.) decreased in OTCs from 2009-2011, and 2009-2016. Evergreen shrub cover increased from 2009-

2011 but decreased overall from 2009-2016. Among non-woody plant lifeforms, forb and graminoid cover decreased from 2009-2016, however graminoid cover increased significantly in OTC's over time. Moss abundance decreased significantly over time and more so within OTC's over the length of this experiment. Although lichen cover increased over time, it decreased in OTC's from 2009-2016. We observed a significant increase in cover of dead plant biomass over time, and a decrease in litter cover from 2009-2016 (Table 5.2).

Trends in growth traits (cover and height) were not always consistent within or among focal species (Appendix 5.2b), however all species exhibited a significant increase in height (cm) within OTCs over time. *Betula glandulosa* cover (%) increased overall from 2009-2016 and within OTC's from 2009-2016. Maximum height (cm) of *B. glandulosa* also increased significantly within OTC's throughout this study. For *V. uliginosum*, we detected a significant increase in cover (%) over time but a decrease within OTCs from 2009-2016. Height (cm) of *V. uliginosum* decreased from 2009-2016 in controls yet increased within OTCs from 2009-2016. We observed significant decreases in *E. nigrum* cover (2009-2011), and height (cm) (2009-2016), however height (cm) increased within OTCs from 2009-2011 and 2016. For *V. vitis-idaea*, cover (%) increased significantly from 2009-2016 yet decreased within OTCs from 2009-2016. Height (cm) of this species increased over the short-term (2009-2011) and within OTCs from 2009-2016 (Table 5.2).

Soil temperature increased significantly from 2011 to 2016 and was higher in OTC's than CTLs. Soil moisture also increased from 2011 to 2016 but was significantly lower in OTC's than CTLs. We found less PAR (%) in OTC's than CTLs, but no change in this parameter over time (Appendix 5.2c). Interaction effects were not significant for any of the microclimate variables in this study (Table 5.2).

5.3.2 Fruit production

The distribution of raw fruit production data (Fig. 5.2) illustrates that the occurrence and abundance of fruit varied greatly among species and between years. Variation was also detected at the site and nested plot levels, as demonstrated by retention of random effects terms for ‘Site’ and ‘PlotID’ for all species (Table 5.3). Regarding focal species growth traits, berry species cover (%) was a significant positive predictor of fruit occurrence and abundance for all species in this study (Table 5.3).

For *V. uliginosum*, we observed no significant effect of experimental warming on fruit occurrence or abundance. The occurrence of fruit increased in the short-term (2009-2011) but decreased by more than 30% from 2009-2016. Cover (%) of this species was a significant positive predictor of fruit occurrence, with greater than 90% probability of fruit when cover values exceeded 40% (Table 5.3; Fig. 5.3, 1a-b). The abundance of *V. uliginosum* fruit declined significantly from 2009-2011, and we found a negative effect of *B. glandulosa* cover on fruit production in this species. Alternatively, cover (%) and height (cm) had a positive effect on fruit abundance in *V. uliginosum* (Table 5.3; Fig. 5.3, 2a-d). When model selection was performed to include microclimatic parameters, soil moisture had a significant negative effect on the abundance of fruit in this species (Appendix 5.3).

The overall occurrence of *E. nigrum* fruit was low in this study (<40%), and it was 15 % lower in controls compared to OTCs. Cover and height were both significant predictors of fruit occurrence in this species, with 60% probability of fruit occurrence when cover and height were > 30% and > 7 cm respectively (Table 5.3; Fig. 5.4, 1a-c). Fruit production declined from 2009-2016 for *E. nigrum,* and cover (%) was the only positive and significant predictor of fruit abundance for this species (Table 5.3; Fig 5.4, 2a-b). When microclimatic parameters were included in model selection, we found a significant and negative effect of experimental warming and soil moisture on *E. nigrum* fruit production (Appendix 5.3).

For *V. vitis-idaea*, we found a short-term (2009-2011) increase in the occurrence of fruit but no significant change in occurrence or abundance over the long term (2009-2016) (Table 5.3; Fig. 5.5, 1e). Fruit production was lower in OTC's than controls; this effect was stronger for this species than *E. nigrum*. We found a negative effect of *B. glandulosa* cover (%) on the occurrence and abundance of *V. vitis-idaea* (Fig. 5.5, 1d, 2b-c). Cover (%) of *V. vitis-idaea* was also detected as positive significant predictor of fruit occurrence and abundance for this species (Table 5.3; Fig. 5.5, 1a, 2a). Unlike *V. uliginosum* and *E. nigrum*, we found no significant effect of soil moisture or other microclimatic parameters on fruit production in this species. However, *V. vitis-idaea* height (cm) was detected as having a significant and positive effect on the occurrence and abundance of fruit in our subset models (Appendix 5.3).

5.4 Discussion

After seven years of experimental warming, we demonstrated a shift towards *B. glandulosa* dominance in the shrub-canopy layer, a loss of bryophyte and lichen cover, and an increase in graminoids at the ground surface layer. All focal berry species grew taller over time within experimental warming plots, but both *Vaccinium* spp. became less abundant, suggesting a phenotypic response to changing resource availability. Although changes in the occurrence and abundance of fruit were species-specific throughout this experiment, we detected a gradient in response to experimental warming whereby fruit production in truly prostrate berry shrubs, *V. vitis-idaea* and *E. nigrum*, was more sensitive to experimental warming than *V. uliginosum*, which is capable of upright growth. *Vaccinium vitis-idaea* was the only species to demonstrate a negative response in fruit occurrence and abundance with increasing *B. glandulosa* abundance, suggesting that fruit production in *V. vitis-idaea* is most vulnerable to tundra shrubification.

5.4.1. Growth Traits and Local Microclimate

Consistent increases in height and cover of *B. glandulosa* over time, and with experimental warming, confirm our prediction that *B. glandulosa* is highly responsive to ambient and experimental warming in Nunatsiavut, Labrador. This result is consistent with our short-term findings from Chapter 4 and with studies tracking deciduous-shrub response to ambient warming throughout eastern Sub-Arctic Canada (Fraser et al. 2011, Tremblay et al. 2012, Ropars et al. 2015b). Negative effects of experimental warming on the ground layer were also as predicted and are consistent with global and regional plot-based studies showing that bryophytes and lichens are most likely to decrease, and graminoids most likely to increase in abundance with experimental warming (Bjorkman et al. 2019, Chagnon and Boudreau 2019). At the current rate of tundra shrubification in Nunatsiavut, positive feedbacks that promote further warming and effects on the ground layer are likely to occur (Vowles and Björk 2019), however there is potential for effects to be mitigated to some extent by ungulate herbivory (Løkken et al. 2019). Although the Eastern Migratory and Torngats caribou populations are at an all-time low throughout Nunavik and Nunatsiavut (COSEWIC 2017), moose are increasing in abundance and distribution along the north coast of Labrador, and are likely to browse on *B. glandulosa* in the absence of more widespread hardwoods and other preferred browse species.

Contrary to our prediction, there was no evidence of a gradient in growth trait response related to phenotypic plasticity with experimental warming among our focal berry species. Plant height is highly responsive to warming across taxa, but it is also strongly affected by moisture availability across sites (Bjorkman et al. 2018). In this study, all focal berry species increased in height with warming from 2009-2016, however both *Vaccinium* spp. decreased in cover in OTC's between 2009-2016. Divergent growth responses within the *Vaccinium* spp. suggest a shift in resource allocation in favour of size over resource economy, potentially in response to increased competition from *B. glandulosa* and/or changing resource availability. Although experimental warming plots were warmer, drier and had less light than controls (as predicted), soil moisture was not limiting (increased from 2011-2016), suggesting that growth traits were more likely affected by interspecific interactions than constrained by abiotic conditions alone.

5.4.2. Fruit Production

Although fruit production was highly variable throughout this study, fruit production declined for all focal berry species from 2009 to 2016 in Nain and Torr Bay, Nunatsiavut (Table 5.3). While this can be explained in part by inter-annual variability (Hupp et al. 2015a, Boulanger-Lapointe et al. 2019b), our models strongly suggest that ambient and experimental warming and *B. glandulosa* cover is constraining fruit production, especially for *V. vitis-idaea,* which has the least phenotypic plasticity in size traits. Taller and more abundant berry shrubs resulted in higher probability and abundance of fruit for all species (especially among those with capacity for upright growth), suggesting that the patterns we observed in growth traits (increased height) did not divert resources away from fruit production in favour of vegetative growth. Although OTC's were warmer, drier, and had less light than control plots, these local (summer) topo-edaphic conditions were not significant predictors of fruit production throughout this study.

Changes in berry resources associated with a taller and denser deciduous shrub canopy may be occurring outside the sample window of this study. For example, tall shrubs are known to trap snow, which can delay snowmelt timing and therefore timing of annual flower production (Anadon-Rosell et al. 2014). In Nunatsiavut where deciduous shrubs are increasing at an accelerated rate, trends in annual snowfall, snowpack persistence and spring warming will be critical in predicting annual berry crops. A taller and denser deciduous shrub canopy will also influence detection and visitation by pollinators which directly affects fruit set in the understory (Scaven and Rafferty 2013).

By mid-century, winter temperatures are expected to increase by more than 7°C in some areas of northern Labrador, accompanied by increased precipitation in the form of rain (especially during winter months) and extensive permafrost thaw (Way et al. 2018, Bush and Lemmen 2019, Government of Newfoundland and Labrador 2019). These projected changes in climate will drive changes in berry resources differently depending on the biophysical and local context. With accelerated warming, flowering times are likely to contract in favour of later-flowering (i.e. *Vaccinium* spp.) over early-flowering (*i.e. E. nigrum*) species (Prevéy et al. 2019). Further warming may continue to drive tundra shrubification in Nunatsiavut (Ju and Masek 2016); however, extreme and winter warming events could also cause shoot mortality and shoot stress throughout the tundra plant communities, leading to “tundra browning” (Phoenix and Bjerke 2016, Treharne et al. 2019). Both processes are likely to result in negative impacts on dwarf berry shrubs, either through a shift in resource allocation from sexual to vegetative regeneration, or though direct damage on shoots and buds.

There is a great deal of uncertainly as to how cryospheric and hydrological change will impact tundra plant communities (Wrona et al. 2016) and therefore berry resources; we suspect impacts on dwarf berry shrubs will range from minor to severe depending on the local context and individual species’ capacity to tolerate and/or resist moisture stress (too much or too little). Ecological monitoring and research are required to determine hydrological-driven constraints on flower and fruit production, particularly in the unique coastal and mountainous climate of Nunatsiavut.

5.4.3 Implications and next steps

Given the consistent negative effect of warming and *B. glandulosa* cover on fruit occurrence and abundance in *V. vitis-idaea*, we suggest that this species, a prostate berry shrub, is (currently) most vulnerable to warming and tundra shrubification in Nunatsiavut. Depending on the geographic scope of tundra shrubification and *V. vitis-idaea*, a decline in this species’ fruit production is likely to have direct and indirect socio-economic implications throughout Nunatsiavut.

Across Inuit Nunangat, berry picking, harvesting and consumption remain culturally and nutritionally relevant for Inuit (Boulanger-Lapointe 2017), and contribute to improved physical and mental wellbeing (Cunsolo Willox et al. 2011, Boulanger-Lapointe et al. 2019b). In Nunatsiavut, berry patches support the food security of residents (Goldhar et al. 2012), while providing small-scale economic benefit for those who harvest to sell throughout the community. Several culturally important wildlife also relies on *V. vitis-idaea* for forage throughout Nunatsiavut. For example, spruce grouse (*Falcipennis canadenis*) and willow ptarmigan (*Lagopus lagopus*) rely on the fruit, buds and leaves of *V. vitis-idaea* (among other ericaceous berry shrubs) to support their spring and summer diet (Johnsgard 2016). This is also the case for Canada geese (*Branta canadensis*) and other migratory birds (Cadieux et al. 2005). Thus, a decline in *V. vitis-idaea* or other dwarf berry shrubs will be felt at multiple levels throughout the regions' food systems.

With this knowledge, there are opportunities and challenges in protecting, managing and potentially restoring berry grounds to maintain availability of this important resource. As a starting point, traditional and scientific knowledge of berry grounds should be mapped throughout Nunatsiavut to determine the geographic scope of the resource, including areas close to communities that are at risk from community expansion and industrial development. Within this scope, areas at risk or already undergoing shrubification could be ranked and prioritized based on their current resource level (annual fruit production and availability) and potential for change. Local and regional governments could use this information to develop an integrated land-use plan, which designates areas for local harvesting only and management. Community-based monitoring of these areas could help track changes in these resources through time. Active management and restoration of shrubified areas is possible yet challenging and not without risk. Restoration options could include exclusion, introduced herbivores, or manual removal among others. Given the extent of global and regional shrubification, these methods are only likely to be feasible at the local scale and for culturally key berry grounds.

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Table 5.1 Climate summary for experimental warming sites located in Nain and Torr Bay, Labrador, Canada

		Decadal climate summaries (2000-2009)*				
Site	Latitude/ Longitude	Mean total annual precipitation (mm)	Mean annual/max./min. temperature (°C)			Degree days > 5° C
Nain	56.54 N 61.69 W	882.5	-1.8	2.4	-6.0	578.6
Torr Bay	58.46 N 62.82 W	791.11*	-5.0*	-0.9*	-9.2*	318.3

*Canadian Climate Normals were only available for our Nain site (http://climate.weather.gc.ca/climate_normals/index_e.html), therefore we calculated decadal climate summaries for each site based on the most recent local data available for both locations (2000-2009). Nain climate summaries were calculated from local station data available through Environment Canada's historical data archive; accessed Feb, 2014 (http://climate.weather.gc.ca/historical_data/search_historic_data_e.html). Torr Bay summaries were derived from gridded monthly mean high resolution (0.5 x 0.5 degree) climate data available from the Climatic Research Unit, Time-Series 3.1 (CRU TS3.1), University of East Anglia CRU, 2011.

Table 5.2 Summary of generalized linear mixed-effects models indicating significant random (‘Site’, ‘PlotID’), fixed (‘Treatment’, ‘Year’) and fixed interaction effects on plant community response and microclimatic conditions. Community response parameters include lifeform cover (%), upright shrub (Begl = *Betula glandulosa*) and berry shrub (Emni = *Empetrum nigrum*; Vaul = *Vaccinium uliginosum*; Vavi = *V. vitis-idaea*) cover (%) and height (cm). Microclimatic response parameters include soil moisture (%), soil temperature (°C), and PAR (%); PAR = photosynthetic active radiation. Coefficients were retained at *p* <0.10. Model statistics represent unstandardized, random intercept only mixed-effects models (Zero truncated; Gamma/Gaussian; identity/log link) with OTC/control pairs (PlotID) nested within Sites (1|Site/PlotID) as random effects terms

	Random factors		**Fixed factors**			**Model performance/selection**	
Community response	**Site**	**Plot ID: Site**	**Treatment (CTL vs OTC)**	**Time (2009, 2011, 2016)**	**Treatment x Time**	**Log likelihood**	**ΔAIC**
Lifeform cover (%)							
Shrubs (all)	X	X	–	↑ (2016)	–	-1049.43	2.7
Deciduous		X	–	↑ (2011; 2016)	–	-977.80	4.5
Upright		X	X	↑ (2016)	↑ (OTC*2016)	-774.18	2.0
Prostrate		X	X	↑ (2011; 2016)	↓ (OTC*2011; OTC*2016)	-893.49	2.0
Evergreen	X	X	–	↓ 2011; ↑ 2016	–	-924.75	2.0
Forbs		X	–	↓ (2016)	–	-259.91	4.0
Graminoids	–	X	X	↓ (2016)	↑ (OTC*2011; OTC*2016)	-430.46	2.0
Lichens	X	X	X	↑ (2011; 2016)	↓ (OTC*2016)	-655.56	NA
Mosses		X	X	↓ (2011; 2016)	↓ (OTC*2011; OTC*2016)	-342.78	2.0
Dead plant biomass	X	X	–	↑ (2011; 2016)	–	-589.66	4.9
Litter	X	X	–	↓ (2011)	–	-864.64	1.9
Upright shrub							

Begl Cover (%)		X	X	↑ (2016)	↑ (OTC*2016)	-779.68	2.0
Max. Begl Height (cm)	X	X	X	X	↑ (OTC*2011; OTC*2016)	-606.85	NA
Berry shrub							
Vaul Cover (%)		X	X	↑ (2011; 2016)	↓ (OTC*2011; OTC*2016)	-890.05	2.0
Vaul Height (cm)	X	X	X	↑ 2011; ↓ 2016	↑ (OTC*2016)	-419.40	NA
Emni Cover (%)		X	–	↓ (2011)	–	-464.37	3.8
Emni Height (cm)		X	X	↓ (2016)	↑ (OTC*2011; OTC*2016)	-163.87	2.0
Vavi Cover (%)		X	X	↑ (2016)	↓ (OTC*2016)	-751.66	2.0
Vavi Height (cm)	X	X	X	↑ (2011)	↑ (OTC*2016)	-324.43	NA
Microclimate							
Soil moisture (%)	X	X	↓	↑ (2011-2016)	–	-473.45	1.2
Soil temperature (°C)	X		↑	↑ (2011-2016)	–	-322.67	3.8
PAR (%)			↓	–	–	-729.8	3.0

***** X denotes when a term was retained in the model; ↑ and ↓ indicate significant direction of change across fixed factors at $p < 0.10$; '–' indicates factors removed during model selection; 'CTL' = control and 'OTC' = open-top warming chamber; $\Delta AIC = AIC_{global} – AIC_{final}$; NA indicates when the global model = AIC_{min}

Table 5.3 Fitted hurdle model summary for the effects of experimental warming and vegetation community attributes on fruit production of a) *Vaccinium uliginosum* (Vaul), b) *Empetrum nigrum* (Emni) and c) *V. vitis-idaea* (Vavi) based on random intercept only mixed-effects hurdle models*.* Random factors included 'Site' and nested 'Plot ID'; Fixed factors included 'Treatment' (OTC vs. CTL), 'Time' (2009, 2011 and 2016), and 'Treatment'*'Time'; Fixed effects included cover and height of each focal berry species and *Betula glandulosa* (Begl). Step 1 summarizes model selection for the probability of fruit production (presence/absence fruit/m^2; binomial error, logit link), and step 2 for the extent of fruit production (total # fruit/m^2; negative-binomial error, log link) for each species. Step 2 coefficients were obtained using standardized (z-score) predictor variables. Coefficients were retained at *p<0.10* (bold). OTC = open-top warming chamber; CTL = control. Δ AIC represents the difference in Akaike Information Criteria (AIC) between the best-fit model and the global model

Berry Shrub	**Hurdle**	**Effects**	**Coefficients/ Intercepts**	**Estimate/ Variance***	**Std. Error/ Std.Dev***	**Z-Value**	**P-Value**	**ΔAIC**	**Log Likelihood**
a. Vaul	**Step 1**	Random	Site	3.69	1.92			3.4	-104.1
			Plot ID	0.22	0.47				
		Fixed	Intercept	0.92	0.46	0.63	0.529		
			Vaul Cover (%)	0.05	0.01	4.15	**<0.001**		
			Year (2011)	0.74	0.43	1.68	0.092		
			Year (2016)	-1.95	0.49	-3.93	**<0.001**		
	Step 2	Random	Site	0.33	0.58			1.6	-732.2
			Plot ID	0.51	0.71				
		Fixed	Intercept	4.92	0.49	9.97	**<0.001**		
			Vaul Cover (%)	0.49	0.15	3.09	**0.002**		
			Vaul Height (cm)	0.36	0.18	1.96	**0.049**		
			Begl Cover (%)	-0.36	0.19	-1.93	**0.053**		

			Year (2011)	-0.68	0.25	-2.66	**0.007**		
			Year (2016)	-0.41	0.34	-1.23	0.219		
b. Emni	**Step 1**	Random	Plot ID	0.62	0.79			6.2	-76.3
		Fixed	Intercept	-3.23	0.62	-5.22	**<0.001**		
			Emni Cover (%)	0.08	0.01	4.56	**<0.001**		
			Emni Height (cm)	0.38	0.09	4.12	**<0.001**		
			Treatment (OTC)	-1.05	0.51	-2.06	**0.040**		
	Step 2	Random	Plot ID	0.63	0.79			5.1	-387.1
		Fixed	Intercept	4.73	0.30	15.40	**<0.001**		
			Emni Cover (%)	0.42	0.16	2.60	**0.009**		
			Year (2011)	-1.50	0.35	-4.06	**<0.001**		
			Year (2016)	-1.65	0.29	-5.69	**<0.001**		
c. Vavi	**Step 1**	Random	Site	4.88	2.21			1.5	-93.3
			Plot ID:Site	0.80	0.89				
		Fixed	Intercept	0.93	1.78	0.52	0.601		
			Vavi Cover (%)	1.03	0.27	3.71	**<0.001**		
			Vavi Height (cm)	0.99	0.40	2.42	**0.015**		
			Begl Cover (%)	-0.61	0.25	-2.40	**0.016**		
			Treatment (OTC)	-0.84	0.48	-1.72	**0.084**		
			Year (2011)	1.65	0.54	3.02	**0.002**		
			Year (2016)	0.63	0.53	1.19	0.233		
	Step 2	Random	Site	0.24	0.49			0.1	-559.4
		Fixed	Intercept	4.93	0.38	12.79	**<0.001**		
			Vavi Cover (%)	0.77	0.14	5.33	**<0.001**		
			Begl Cover (%)	-0.32	0.12	-2.72	**0.006**		
			Treatment OTC	-0.60	0.23	-2.62	**0.008**		

Fig. 5.1 Map of Newfoundland and Labrador identifying study site locations, Nain and Torr Bay, along the north coast of Nunatsiavut, northern Labrador, Canada. Map modified from d-maps.com. (https://dmaps.com/m/america/canada/newfoundland/newfoundland11.gif)

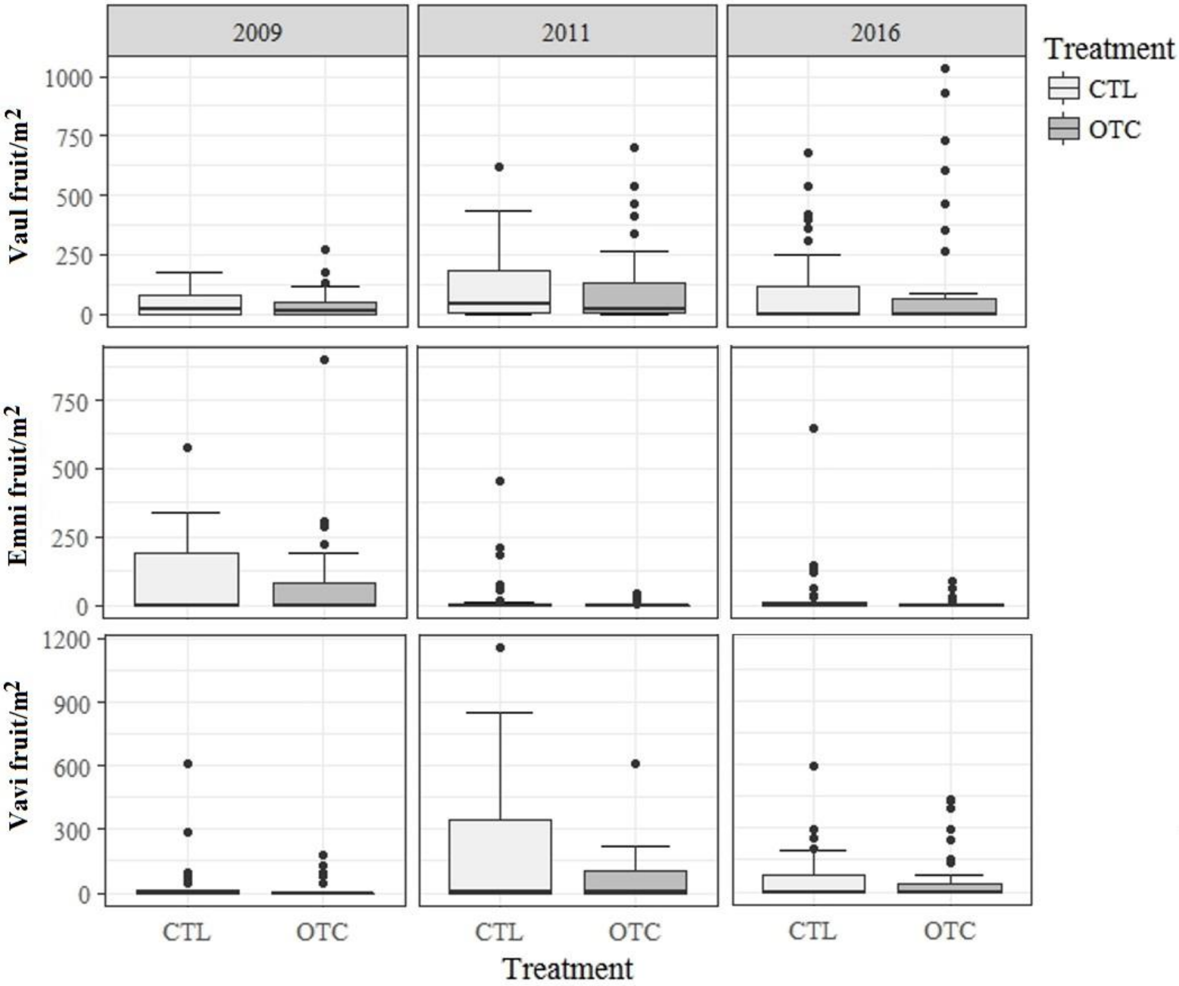


Fig. 5.2 Boxplots illustrating fruit production (total #fruit/m^2) (median, interquartile range, min/max and outliers) of *Vaccinium uliginosum* (Vaul), *Empetrum nigrum* (Emni) and *V. vitis-idaea* (Vavi) between controls (CTL) and open-top warming chambers (OTC) over three sample periods in Nain and Torr Bay, Nunatsiavut Labrador.

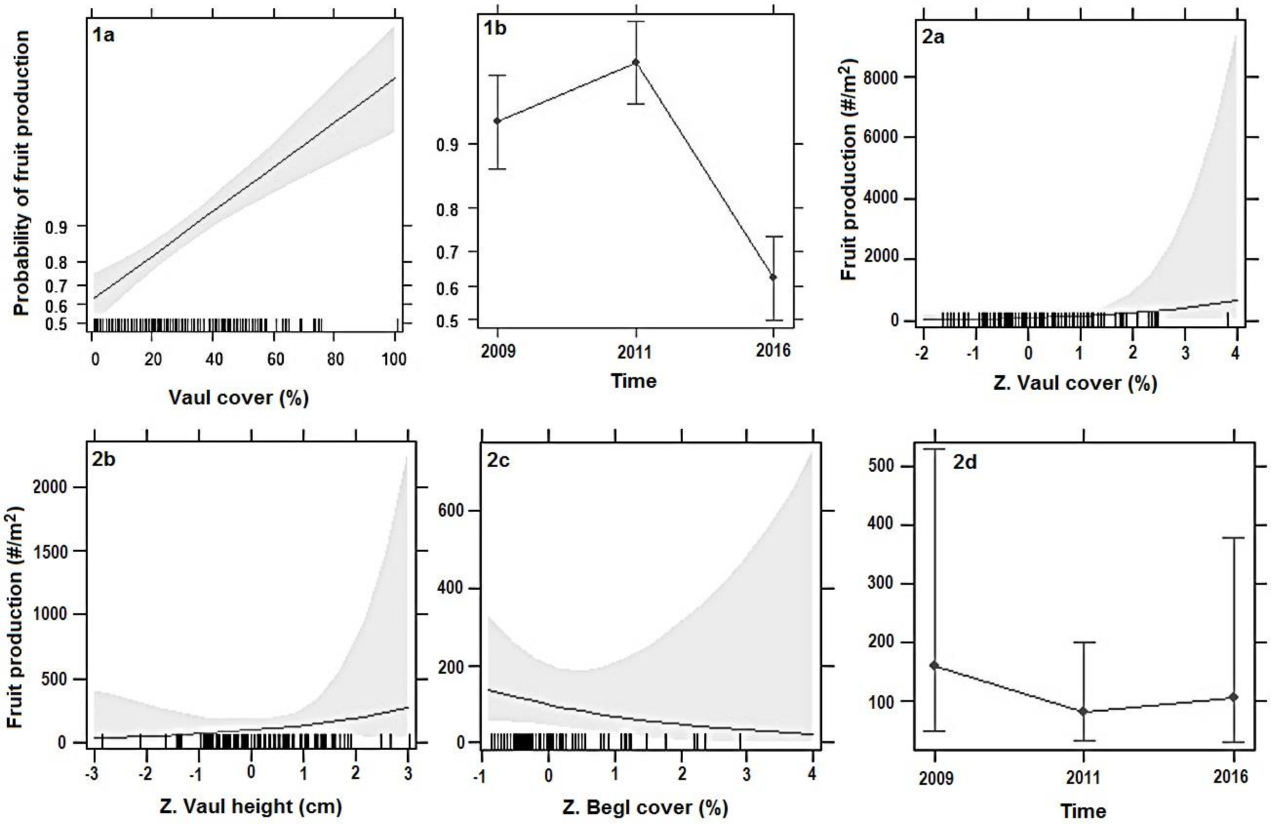


Fig. 5.3 Fixed effect plots indicating the magnitude and strength of significant parameter effects on the probability (1a-b) and extent (2a-d) of fruit production in *Vaccinium uliginosum* (Vaul), as determined by generalized linear mixed-effects hurdle models summarized in Table 5.3. Shaded areas represent 95% confidence intervals; Error bars = standard error; CTL = control, OTC = open-top warming chamber, Begl = *Betula glandulosa*; Black lines along x-axis represent raw (1a) and standardized (2a-c) observations.

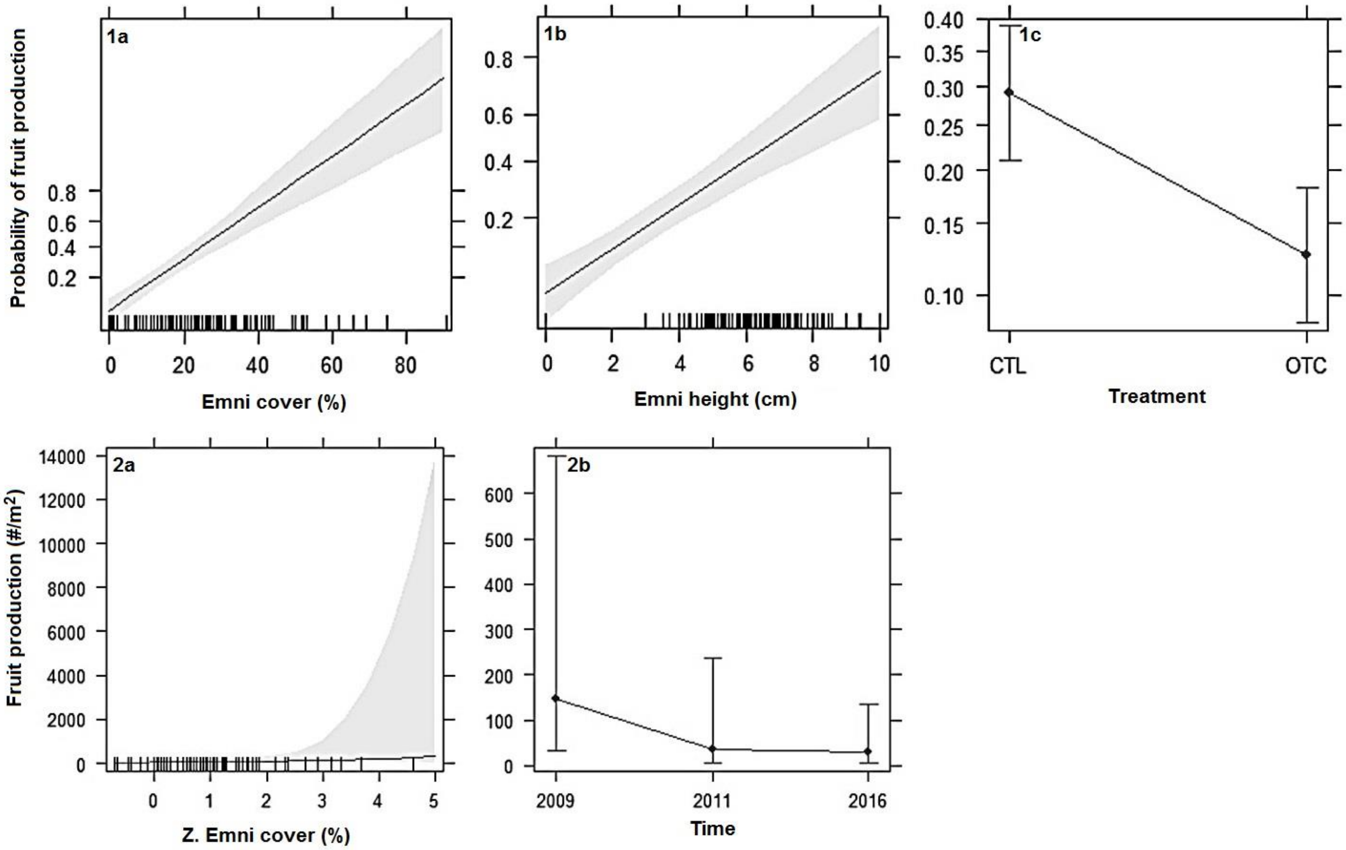


Fig. 5.4 Fixed effect plots indicating the magnitude and strength of significant parameter effects on the probability (1a-c) and extent (2a-b) of fruit production in *Empetrum nigrum* (Emni), as determined by generalized linear mixed-effects hurdle models summarized in Table 5.3. Shaded areas represent 95% confidence intervals; Error bars = standard error; CTL = control and OTC = open-top warming chamber; Black lines along x-axis represent raw (1a-b) and standardized (2a) observations.

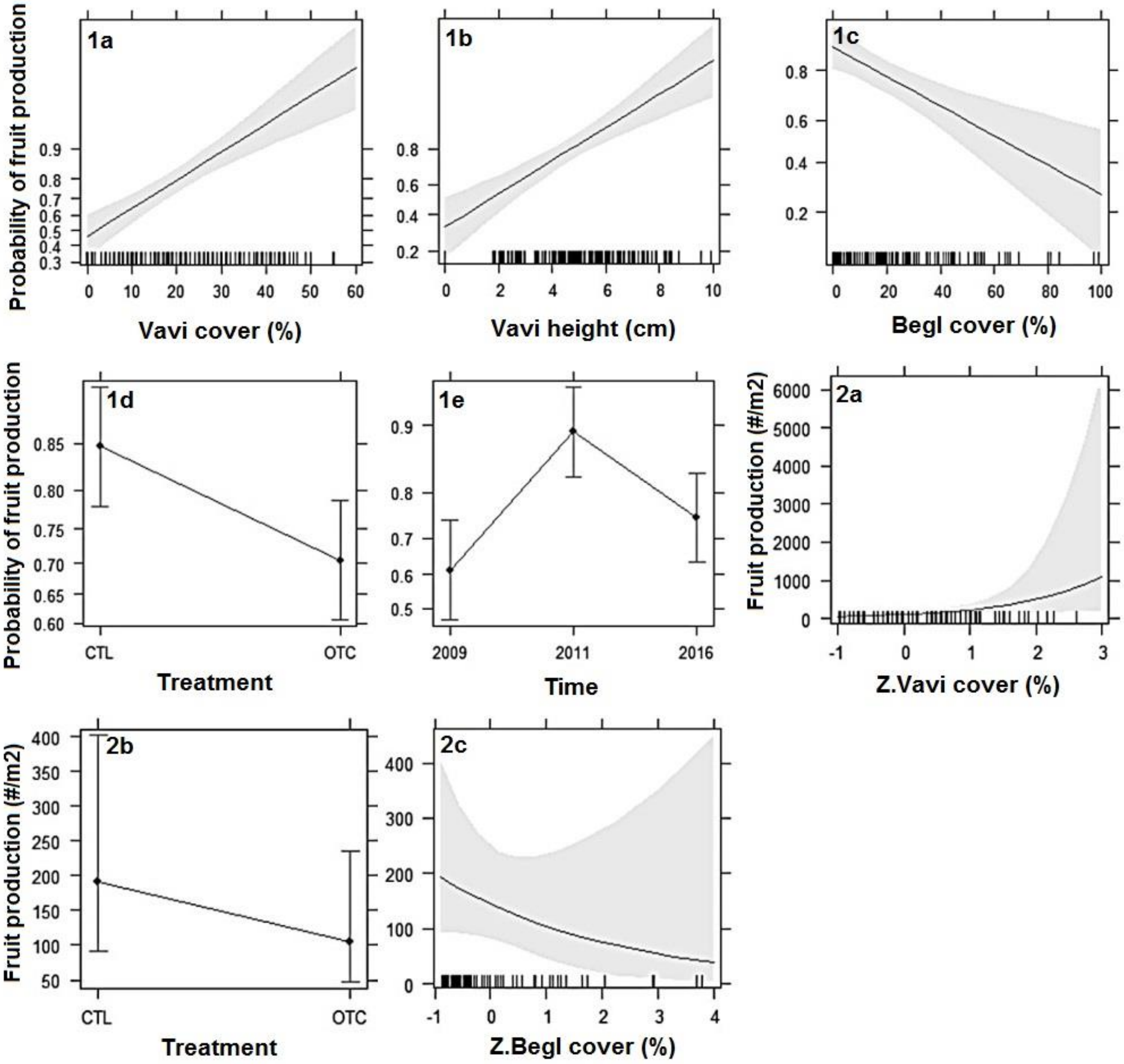


Fig. 5.5 Fixed effect plots indicating the magnitude and strength of significant parameter effects on the probability (1a-e) and extent (2a-c) of fruit production in *Vaccinium vitis-idaea* (Vavi), as determined by generalized linear mixed-effects hurdle models summarized in Table 5.3. Shaded areas represent 95% confidence intervals; Error bars = standard error; CTL = control, OTC = open-top warming chamber, Begl = *Betula glandulosa*; Black lines along x-axis represent raw (1a-c) and standardized (2a,c) observations.

Appendix 5.1 R-code for generalized linear mixed hurdle models using packages ‘MASS’ (Venables and Ripley 2002), lme4 (Bates et al. 2015), glmmADMB (Bolker et al. 2013), and ‘effects’ (Fox 2003).

Hurdle Step 1:

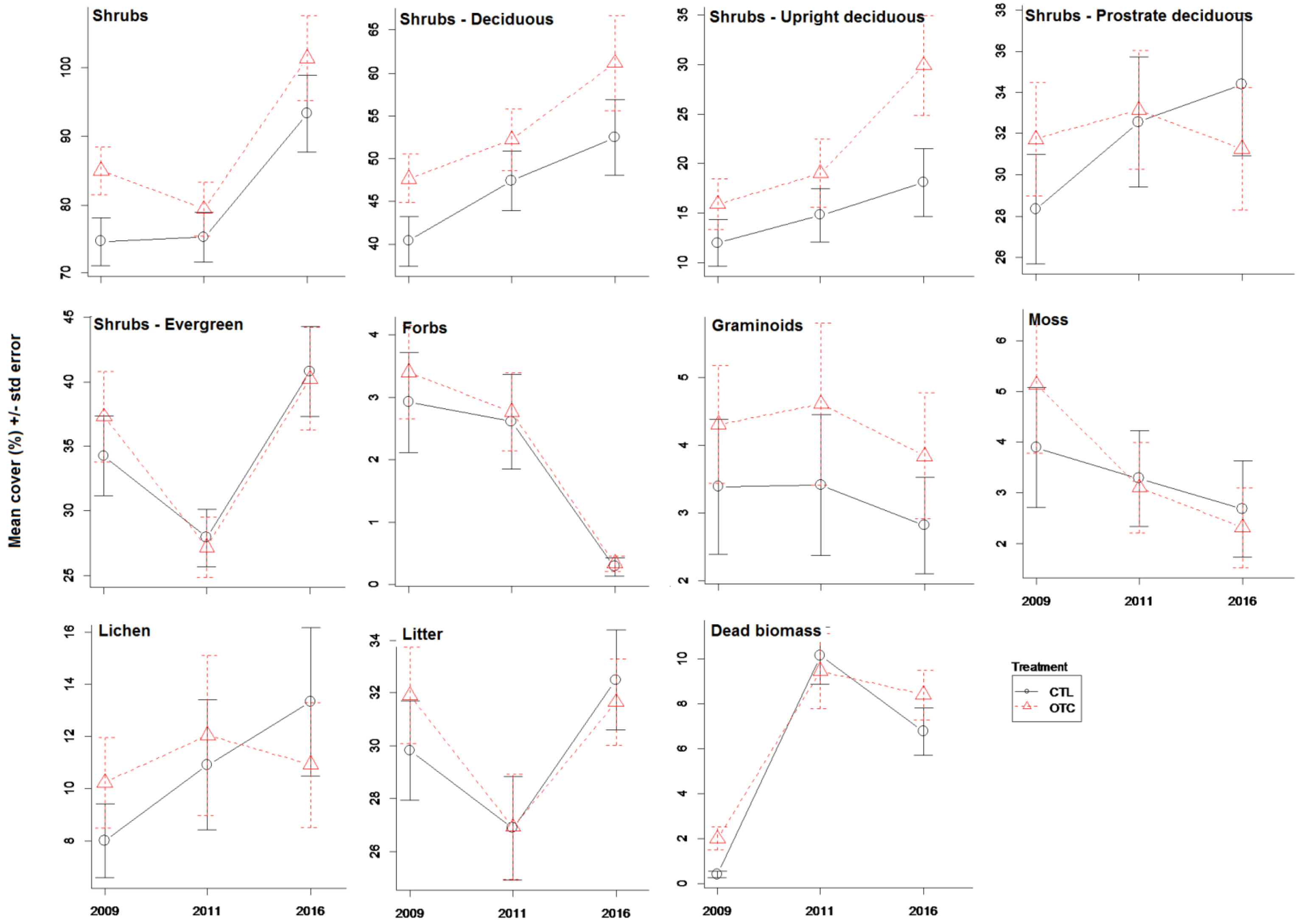
```
>library(lme4)
>ModelName<glmer(Y~(1|Site/PlotID) + X1 +Xx +…..Xz + (X1*Xx), na.action=na.omit,
data = , family="binomial")
```

Hurdle Step 2:

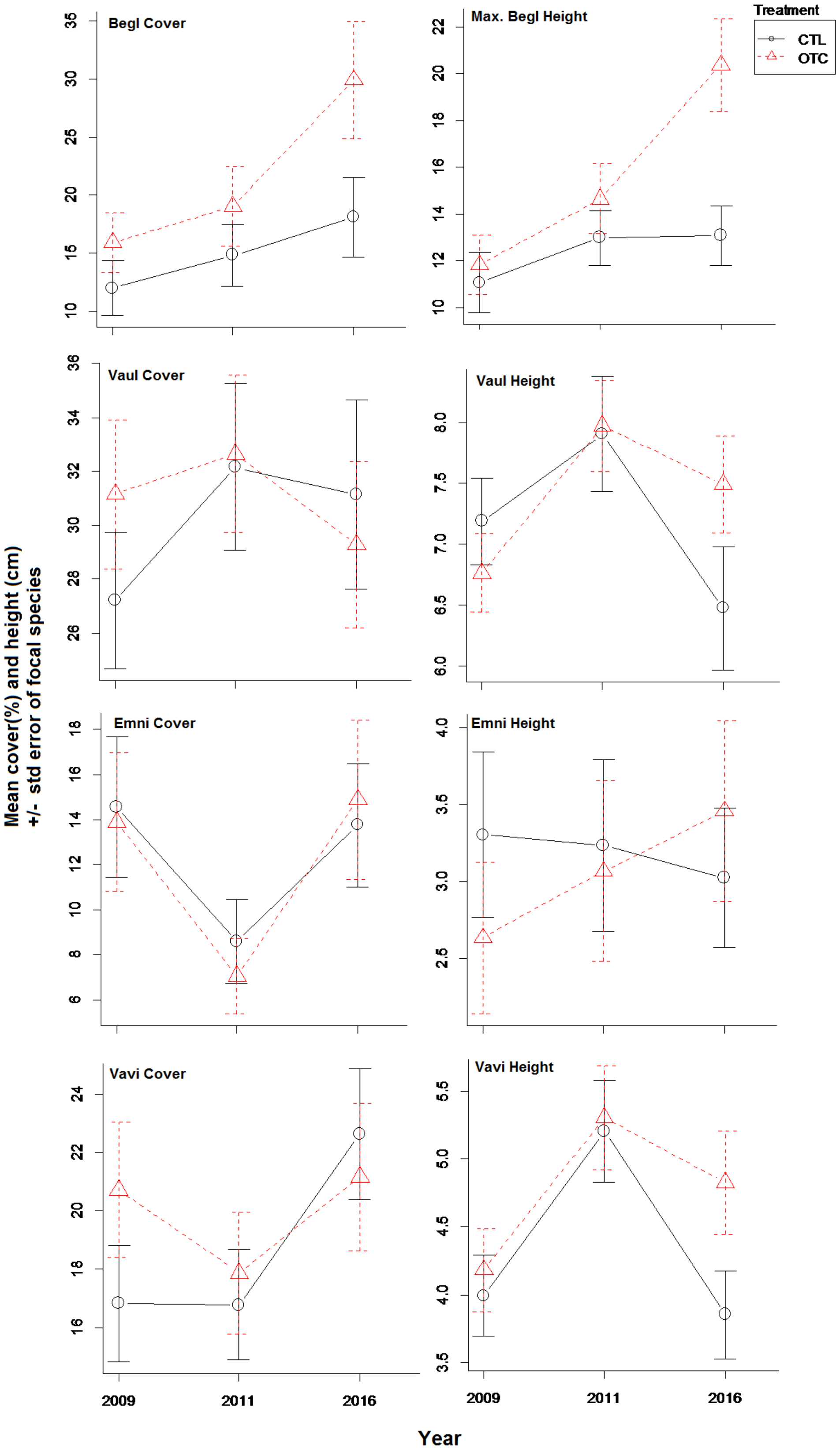
```
>library(glmmADMB)
>ModelName<glmmadmb(Y~(1|Site/PlotID)+ X1 +Xx +…..Xz + (X1*Xx), family="nbinom",
data = subset(, Y > 0))
```

Effects Displays:

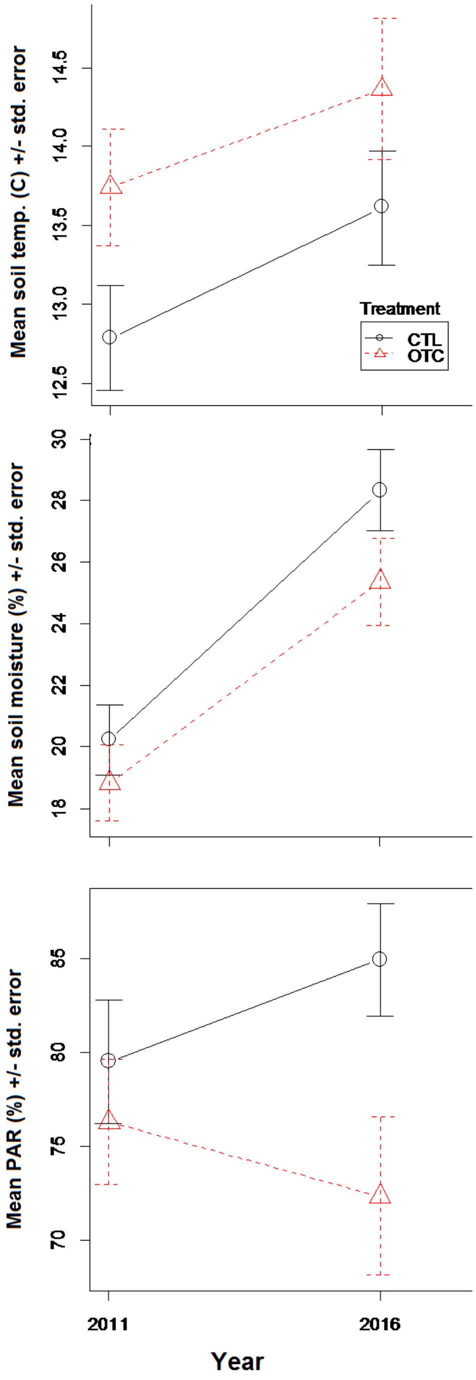
```
>library(effects)
> plot(allEffects(model),rescale.axis=FALSE)
```



Appendix 5.2a Means and standard error of lifeform cover from 2009-2016 between controls (CTL) and experimental warming (OTC) treatments.


Treatment
CTL
OTC
Begl Cover
10
15
20
25
30
35
Max. Begl Height
10
12
14
16
18
20
22
Vaul Cover
26
28
30
32
34
36
Vaul Height
6.0
6.5
7.0
7.5
8.0
Emni Cover
6
8
10
12
14
16
18
Emni Height
2.5
3.0
3.5
4.0
Vavi Cover
16
18
20
22
24
Vavi Height
3.5
4.0
4.5
5.0
5.5
2009
2011
2016
Mean cover(%) and height (cm)
+/- std error of focal species
Year

Appendix 5.2b Means and standard error of focal species cover (%) and height(cm) from 2009-2016 between controls (CTL) and experimental warming (OTC) treatments. Begl = *Betula glandulosa*; Emni = *Empetrum nigrum*; Vaul = *Vaccinium uliginosum*; Vavi = *V. vitis-idaea.*



Appendix 5.2c Means and standard error of Soil temperature (°C), % Moisture and %PAR from 2009-2016 between controls (CTL) and experimental warming (OTC) treatments.

Appendix 5.3 Fitted hurdle model summary for the effects of experimental warming, vegetation community attributes and plot-level microclimate on fruit production of a) *Vaccinium uliginosum* (Vaul), b) *Empetrum nigrum* (Emni) and c) *V. vitis-idaea* (Vavi) based on random intercept only mixed-effects hurdle models. Random factors included 'Site' and nested 'Plot ID'; Fixed factors included 'Treatment' (OTC vs. CTL), 'Time' (2011 and 2016), and 'Treatment'*'Time'; Fixed effects included cover and height of each focal berry species and *Betula glandulosa* (Begl), and local climate variables (Soil moisture (%), Soil temperature (°C), and PAR (%); PAR = photosynthetic active radiation). Step 1 summarizes model selection for the probability of fruit production (presence/absence fruit/m^2; binomial error, logit link), and step 2 for the extent of fruit production (total # fruit/m^2; negative-binomial error, log link) for each species. Step 2 coefficients were obtained using standardized (z-score) predictor variables. Coefficients were retained at *p* <0.10. OTC = open-top warming chamber; CTL = control. Δ AIC represents the difference in Akaike Information Criteria (AIC) between the best-fit model and the global model.

Berry Shrub	**Hurdle**	**Effects**	**Coefficients/ Intercepts**	**Estimate/ Variance***	**Std. Error/ Std.Dev***	**Z-Value**	**P-Value**	**ΔAIC**	**Log Likelihood**
a. Vaul	**Step 1**	Random	Site	4.30	2.07			4.5	-60.6
		Fixed	Intercept	1.74	1.60	1.08	0.278		
			Vaul Cover (%)	0.07	0.01	4.41	<0.001		
			Begl Cover (%)	-0.02	0.01	-1.81	0.070		
			Year (2016)	-2.69	0.53	-5.00	<0.001		
	Step 2	Random	PlotID	0.85	0.92			7.2	-536.6
		Fixed	Intercept	3.56	0.22	16.18	<0.001		
			Vaul Cover (%)	0.44	0.18	2.41	0.016		
			Vaul Height (cm)	0.70	0.21	3.34	<0.001		
			Begl Cover (%)	-0.65	0.23	-2.79	0.005		

			Moisture (%)	-0.50	0.19	-2.32	0.020		
			Year (2016)	0.76	0.27	2.82	0.004		
b. Emni	**Step 1**	Random	Plot ID	4.54	2.13			5.2	-54.9
		Fixed	Intercept	-4.20	1.41	-2.97	0.003		
			Emni Cover (%)	0.10	0.04	2.60	0.009		
			Emni Height (cm)	0.53	0.19	2.83	0.005		
			Treatment (OTC)	-2.22	1.10	-2.01	0.044		
	Step 2	Random	Plot ID	0.50	0.71			11.1	-214.3
		Fixed	Intercept	3.56	0.36	9.71	<0.001		
			Emni Cover (%)	0.65	0.18	3.54	<0.001		
			Max. Begl Height (cm)	0.58	0.26	2.25	0.024		
			Moisture (%)	-0.45	0.23	-1.97	0.049		
			Treatment (OTC)	-1.17	0.44	-2.64	0.008		
c. Vavi	**Step 1**	Random	Site	3.30	1.82			6.0	-68.7
			Plot ID:Site	0.62	0.78				
		Fixed	Intercept	-1.93	1.75	-1.10	0.270		
			Vavi Cover (%)	0.06	0.02	2.92	0.003		
			Vavi Height (cm)	0.59	0.20	2.89	0.003		
			Begl Cover (%)	-0.03	0.01	-2.58	0.010		
	Step 2	Random	Site	0.02	0.13			5.4	-473.6
			PlotID	0.10	0.32				
		Fixed	Intercept	4.36	0.42	10.48	<0.001		
			Vavi Cover (%)	0.67	0.19	3.54	<0.001		
			Vavi Height (cm)	0.86	0.41	2.14	0.032		
			Begl Cover (%)	-0.44	0.16	-2.79	0.005		
			Treatment OTC	-0.74	0.32	-2.28	0.023		

Chapter 6: Summary and conclusions

Predicting climate-driven changes in tundra berry resources is necessary to understand the scale, extent and severity of impacts on this resource, to support ongoing and future land-use planning, and to implement climate change adaptation and mitigation strategies that are locally relevant across Inuit regions of Canada. In this study, we establish multiple lines of evidence to show that although berry resources are highly variable, there are important ecological and trait-based relationships that guide our understanding of future impacts.

By bringing together the richness of Inuit observations of climate change with 30-year trends in local climate variables across communities (Chapter 2), this study identified pan-Canadian Arctic, regional and local-scale patterns in how environmental change is experienced across the Canadian Arctic. By using a new and integrated approach to visualize patterns in the relationship between participant observations and climate records, annual, fall and spring precipitation were identified as potential drivers for some of the observed changes. Inuit TEK brought to light new insights on changes in shrub, plant and insect abundance, and identified shrub expansion as a potential mechanism for declining berry quantity and quality in Nain, Labrador. Collectively, these results underscore the necessity for place-based and Indigenous knowledge in climate change adaptation response initiatives.

In Chapter 3, we utilized the ecological gradients in abiotic resources and species relationships across the forest-tundra ecotone in Nain, Labrador to understand the role of canopy-understory interactions in dwarf berry shrub growth and fruit production. Using a combination of ordination and hurdle models, we found that berry shrub performance differentiated most strongly among species at the interface between the lower and upper forest-tundra transition zone, where boreal and tundra elements diverge, corresponding to an increase in available light and other aboveground resources. Closed-canopy forest had consistent negative effects on the extent of fruit production for all berry species. Positive growth-reproduction relationships were exhibited for both *Vaccinium* species, indicating the importance of abundance as a growth trait in reproductive allocation of *Vaccinium*. We identified that different abiotic and biotic factors are important in explaining the presence vs. extent of fruit production for all species; a distinction realized through the application of hurdle models. By documenting strong canopy-understory feedbacks on growth and fruit production of dwarf berry shrubs at treeline, this study supports traditional and scientific predictions that expansion of tree and tall-shrub canopy could reduce fruit production and therefore availability of fruit across low shrub tundra ecosystems.

Building on what we learned about the importance of local factors in driving changes in tundra resources (Chapter 2), and the role that canopy dynamics play in mediating dwarf berry shrub performance, we brought together experimental warming studies from five geographic locations in eastern Low and Sub-Arctic Canada to examine short-term effects of experimental warming and upright deciduous shrub growth (tundra canopy-formers) on the growth and fruit production of three culturally-relevant tundra berry species (Chapter 4). In two and three years, we demonstrated the responsiveness of *B. glandulosa* height to warming and showed that fruit production in prostrate berry shrubs (*V. vitis-idaea* and *E. nigrum*) is more sensitive to warming and deciduous shrub height than berry species (*V. uliginosum*) with height plasticity.

Warming reduced reproductive effort and success in *E. nigrum*, but mainly reproductive success in *V. vitis-idaea*. Overall, fruit production varied greatly at the site and/or plot level, suggesting strong local drivers on fruit production across the eastern Low and Sub-Arctic region, especially for *V. vitis-idaea*. Divergent responses among prostrate berry shrubs to *B. glandulosa* height suggest a gradient in competitive and facilitative interactions among species. This study demonstrates the potential for future warming and shrubification to constrain fruit production of culturally important prostrate berry shrubs at the regional scale.

In Chapter 5, we recognize that growth-reproduction relationships may vary among species through time and with local topo-edaphic conditions, therefore we follow the effects of experimental warming in our eastern Sub-Arctic Labrador sites from 2009 to 2016; a region with TEK of declines in berry resources and rapid expansion from upright deciduous shrubs. All focal berry species grew taller over time within experimental warming plots, however *Vaccinium* spp. also became less abundant, suggesting a phenotypic response to changing resource availability. Changes in the occurrence and abundance of fruit were species-specific throughout this experiment, and we detected a gradient in response to experimental warming whereby fruit production in truly prostrate berry shrubs, *V. vitis-idaea* and *E. nigrum*, was more sensitive to experimental warming than *V. uliginosum*, which is capable of upright growth. Inclusion of local topo-edaphic variables from 2011 to 2016 enabled us to identify that conditions are becoming warmer and drier in our warming experiments, however effects of these changes on fruit production were marginal in the observed timeframe. *Vaccinium vitis-idaea* was the only species to demonstrate a negative response in fruit occurrence and abundance with increasing *B. glandulosa* abundance, suggesting that fruit production in *V. vitis-idaea* is most vulnerable to tundra shrubification.

In this study, we advanced our understanding of climate change impacts on tundra berry resources by demonstrating that fruit production in culturally important prostrate dwarf berry shrubs, especially *V. vitis-idaea*, is at greater risk of decline from current and future shrubification than berry shrubs with greater phenotypic variation in growth traits. Although changes in berry resources are widespread and consistent across regions such as eastern Sub-Arctic Canada, traditional and scientific knowledge of local conditions is essential to predict meaningful impacts.

Berry resources in eastern Sub-Arctic Canada are at risk of decline from accelerated warming and deciduous shrub expansion. We recommend that local communities and regional governments identify priority berry picking grounds and take these areas into consideration when land-use planning for future use of berry resources and to ensure food security. Tundra shrubification is neither uniform in space nor time, therefore site-based assessments of vulnerability and risk to shrub expansion will be required to evaluate appropriate adaptation response strategies that meet the needs of communities.