# Hierarchies of habitat: Diapensia lapponica on the Avalon Peninsula

by © Heather Baehre

A thesis submitted to the

School of Graduate Studies

in partial fulfillment of the requirement for the degree of

**Master of Science** 

**Department of Geography** 

Memorial University of Newfoundland

October 2022

St. Johns's, Newfoundland and Labrador

#### Abstract

Arctic-alpine flora are known for their resilience to the selective pressures of their associated climate, glacial history, and geology. The coastal barrens of the Avalon Peninsula of Newfoundland are a unique region with arctic-alpine flora, best demonstrated by the persistence of arctic-alpine species, Diapensia lapponica, yet occur at low elevation within a temperate climate. This thesis examines their functioning and persistence within the local plant communities from a hierarchical perspective aiding in interpretations of the species range on a regional scale. Our results show that D. lapponica is capable of ameliorating extreme temperatures over the course of the warmest and coldest months on the Avalon Peninsula, which suggests it has an important role as a microhabitat provider for species less resilient to the environmental conditions. On a local scale, we found that D. lapponica exists in a habitat with a very specific set of requirements for persistence including high ground, and relatively low to medium species diversity including those that are generally slow-growing species and are unlikely to be highly competitive. We also compared this plant community to other locations regionally across eastern North America. Here, we found that the plant communities associated with the presence of *D. lapponica* follow latitudinal and elevational gradients. This research provides important empirical findings on the association of ground cover, microtopography, and microclimate with the way that *D. lapponica* persists on the Avalon Peninsula which can help to inform future conservation and management of these populations on the island.

Keywords: arctic-alpine flora, microclimate, coastal barrens, microhabitat, *Diapensia lapponica*, community composition

#### Acknowledgements

I would first like to express my immense gratitude to my supervisor, Dr. Carissa Brown, for her unwavering support throughout my program. Without your patience and compassion during personally and academically challenging times, it is unlikely I would have made my way to the finish line, especially when the journey was so meandering. I would like to thank you for sharing your wonderful knowledge and extensive skill set of ecology that has provided me with the guidance and tools I will bring with me into my next chapter of life. You have shown me what it means to be a present, encouraging, and honest supervisor which I will always remember if I am ever in a role where I am guiding others. Finally, I must thank you for fostering my love of weird, wonderful, and resilient plants that I would have never found had I not met you.

I would also like to thank my committee member, Dr. Norm Catto, whose valuable, almost immediate feedback, and wealth of knowledge of the Avalon Peninsula and the island of Newfoundland provided me with perspective on my project that improved it immensely. Your support and patience were greatly appreciated.

I also extend my gratitude to the individuals who contributed their botanical knowledge of arctic-alpine species and provided what data or information they had available to my eastern North American comparative study. Paul Sokoloff (Canadian Museum of Nature), Zoe Panchen (University of British Columbia), Sergei Ponomarenko (Canadian Museum of Nature), Anna Crofts (Université de Sherbrooke and formerly Memorial University), and Georgia Murray (Appalachian Mountain Club) – thank you, your help and inspiration was appreciated more than you know. A special thank you to Nathalie Djan-Chékar from The Rooms Museum in St. John's, NL for allowing me to use the resources the collections had to offer and sharing her wealth of knowledge.

iii

I am grateful for my lab mates and colleagues over the course of my program for always being willing to share knowledge and expertise, commiserate, or just have a laugh. Your support, empathy, and time have been vital in my progress, and it means more than you know given how busy you all were with your own projects and endeavors. A special thank you to my wonderful field assistants; Jennifer Sullivan, Bella Richmond, Kirsten Reid, Erin Pearson, and Adam Meyer who donated hours of their time and the utmost patience to brave the RDF and wind on the barrens of the Avalon Peninsula to chase tiny, cute plants and lay transects that had to be held down by rocks. Without all of you, this project would not have been possible.

I am also so incredibly thankful for my partner, Brandon, whose support, and patience have been tireless. Thank you for talking me through my doubts and having confidence in my abilities even when I lacked it myself –this will forever be a gift. I am also grateful for your help as my field assistant on the last day of my field work even if you lucked out and experienced no wind or rain – I guess I should have brought you out sooner. Thank you for being by my side through all of it and providing thoughtfulness and perspective always.

Finally, I will be forever grateful for my amazing family who have been cheering me on and sending love from afar every step of the way and been so excited to see each bit of progress made. A special thank you to my dad, Ralph, for contributing his GIS knowledge and expertise to help me with my maps in the homestretch – your patience was much appreciated. I am also incredibly thankful for Brandon's family who have provided me with support and kindness over the last few years and certainly made being far from my own family during ups and downs more bearable. I feel privileged to have such a wonderful community of people that I call family, near and far.

iv

# Land acknowledgement

I would like to respectfully acknowledge the territory in which this study took place as the ancestral homelands of the Beothuk, and the island of Newfoundland as the ancestral homelands of the Mi'kmaq and Beothuk.

# **Table of Contents**

Abstract	•••••		ii
Acknowledg	gements .		iii
Table of Co	ntents		vi
List of Table	es		viii
List of Figur	res		ix
Chapter 1: 1	[ntroduc	tion and thesis overview	
1.1	Introd	luction	1
1.2	Diape	ensia lapponica life history and ecology	
1.3	Study	Region	5
	1.3.1	Study Sites	5
	1.3.2	Geology and soils of the Avalon Peninsula	
	1.3.3	Protected Areas and Human Activities	
1.4	Previ	ous Research and Thesis Objectives	15
1.5	Thesi	s organization	
1.6	Refer	ences	
Chapter 2: 1	Hierarch	ies of Habitat: <i>Diapensia lapponica</i> on the Avalon Peninsula	
2.1	Introd	luction	
2.2	Metho	ods	
	2.2.1	Study area	
	2.2.2	Field methods	
		2.2.2.1 Community composition of the Avalon Peninsula	
		2.2.2.2 Microtopgraphy	
		2.2.2.3 Microclimate	
		2.2.2.4 Community Composition for eastern North America	
	223	Statistical analyses	30
	2.2.3	2.2.3.1 Community Composition of the Avalon Peninsula	
		2.2.3.2 Community Composition for eastern North America	
2.3	Resul	ts	
2.0	2.3.1	Cushion-level characteristics	
		2.3.1.1 Microclimate	
	222	Community-level characteristics	3/
	2.3.2	2.3.2.1 Community composition and population characteristics	on the
		Avalon Peninsula	34
		2322 Microtonography	26
		2.5.2.2 microrography	

	2.3.3 Regional-level characteristics		
	2.3.3.1 Community composition of eastern North America		
2.4	Discussion		
	2.4.1 Cushion-scale characteristics		
	2.4.2 Community-scale characteristics		
	2.4.3 Regional-scale characteristics		
	2.4.4 The future of <i>D. lapponica</i> on the Avalon Peninsula		
	2.4.5 Conclusions	50	
2.5	References		
Chapter 3: Su	ummary and conclusions		
3.1	Summary of findings		
3.2	Implication of findings		
3.3	Study considerations and limitations		
3.4	Future study suggestions		
3.5	Recommendations for management		
3.6	Conclusion		
3.7	References	67	
Appendix			

#### **List of Tables**

# List of Figures

Figure 1.1. Adapted cross-section diagram of <i>D. lapponica</i> showing the A: inner dead leaf
matter; B: densely packed outer living leaves; C: thin branches; D: main stem (Scott and Day,
1981)
Figure 1.2. Cross-section of live <i>D. lapponica</i> cushion (approx. 9 cm diameter) at Hawke Hills
Ecological Reserve, NL in September 2019. Scale 1:1.5 (Photo: Baehre, 2019)
Figure 1.3. D. lapponica flowering (A) alongside an empty peduncle (C) and colour change
from green to dark burgundy beginning to occur in leaves (B) during August 2020 at Hawke
Hills, NL. Scale 1:1 (Photo: Baehre, 2020)
Figure 1.4. Map of the Avalon Peninsula, Newfoundland, Canada with Hawke Hills and Avalon
Wilderness Reserve sites. (Map Credit: Ralph Baehre, 2022)
Figure 1.5. Map of Hawke Hills study sites surveyed between September 2019 and October
2020 located on the Avalon Peninsula, Newfoundland, Canada. (Map Credit: Ralph Baehre,
2022)
Figure 1.6. Map of South West Pond (Avalon Wilderness Reserve) study sites surveyed between
September 2019 and October 2020 located on the Avalon Peninsula, Newfoundland, Canada.
(Map Credit: Ralph Baehre, 2022) 11
Figure 2. 1. Study design for assessing plant community composition associated with D.
lapponica (blue) and microtopography features (red) at three sites in the Hawke Hills and two
sites in the Avalon Wilderness Reserve
Figure 2. 2. Microtopography features in relation to one another on the Avalon Peninsula, island
of Newfoundland

Figure 2. 3. Demonstration of the four microtopography features; A. Crevice, B. Flat, C. Mat, D.
Mound, observed on the Avalon Peninsula during field surveys in Fall 2020
Figure 2. 4. iButton Thermochron temperature loggers inserted below D. lapponica cushion (top
left) and below ground cover approximately 2.5-3 cm (bottom right)
Figure 2. 5. Average temperatures (°C) of internal cushion (red) and exposed (blue) ground at
Hawke Hill Ecological Reserve (n= 15) and South West Pond (Avalon Wilderness Reserve)
(n=10) sites between November 2019 and August 2020
Figure 2. 6. Average temperatures (°C) of internal cushion and exposed ground between
November 2019 and August 2020
Figure 2. 7. Maximum temperatures (°C) of internal cushion and exposed ground between
November 2019 and August 2020
Figure 2. 8. Minimum temperatures (°C) of internal cushion and exposed ground between
November 2019 and August 2020
Figure 2. 9. Non-metric multidimensional scaling (NMDS) plot describing the community
composition of surveyed sites at Hawke Hill Ecological Reserve and South West Pond (Avalon
Wilderness Reserve) on the Avalon Peninsula of Newfoundland. The turquoise and green convex
hulls indicate the clusters of communities where D. lapponica is most commonly present or
absent, respectively. Each point represents a ground cover community observed in a $1m^2$ quadrat.
NMDS diagrams show similarities (or dissimilarities) of communities based on the distance
between points. The farther apart the points are, the more dissimilar the communities are and
vice versa

Figure 2. 10. Plot demonstrating the influence of the interaction between the number of vascular
plant species and percent rock cover on percent cover of D. lapponica. Light blue shaded area
represents the standard error
Figure 2. 11. Number of <i>D. lapponica</i> individuals observed across four microtopographical
features (crevice, flat, mat, mound) at two sites near South West Pond (Avalon Wilderness
Reserve) and three sites in the Hawke Hills on the Avalon Peninsula, NL in Fall 2020
Figure 2. 12. Proportion (%) of D. lapponica observed on three types of ground cover (rock,
vegetation, or vegetation and rock mix) across four microtopographical features (crevice, flat,
mat, mound) on the Avalon Peninsula, NL between Fall 2020
Figure 2. 13. Proportion (%) of D. lapponica across four microtopographical features (crevice,
flat, mat, mound) and proportion (%) of each of the four microtopographical features across the
microtopographical landscape on the Avalon Peninsula, NL in Fall 2020
Figure 2. 14. NMDS of composition for communities where <i>D. lapponica</i> is present in other
Eastern North American locations. Ordination diagrams show similarities (or dissimilarities) of
communities based on the distance between points. The further apart the points are, the more
dissimilar the communities are and vice versa. Overlain blue vectors represent environmental
factors such as latitude and elevation (included in this figure) that may drive the plant
communities where the directional arrow trends towards
Figure 2. 15. Example of incidentally observed species within the dead and living tissue of D.
lapponica. Species include K. angustifolia, S. tridentata, V. vitis-idaea, fruticose lichen, and
grasses
Figure 2. 16. Typical Hawke Hills site

 Figure 2. 17. Typical Avalon Wilderness Reserve site on top of an outcrop overlooking South

 West Pond often surrounded by lowlands of balsam fir and eastern larch forests, as well as

 wetland.
 47

# **Co-Authorship Statement**

Dr. Carissa Brown is a co-author on all chapters of this thesis. As the primary author, I have been the primary researcher of the study for the literature review, designing the research proposal, project planning and logistics, fieldwork, laboratory work, data analysis, and manuscript preparation. All parts of the project were done in collaboration with Carissa Brown who provided significant contributions to project design, data analysis, and manuscript preparations.

#### **Chapter 1: Introduction and thesis overview**

## **1.1 Introduction**

Alpine communities are being threatened under climate change. Increasing temperatures and alterations in climate patterns are resulting in the encroachment of lower elevation and invasive species (Cavieres et al., 2007; Kudo et al., 2017). Changes in community assemblage will alter biotic interactions such as competition and facilitation (Callaway, 2007; Cavieres et al., 2014; Jägerbrand et al., 2009). As well, although changing climatic conditions may provide more ideal conditions for these lower elevation species to advance upslope, high alpine species that are unable to advance much further due to local topography, therefore, have nowhere to go (Graae et al., 2018; Klanderud & Totland, 2007).

In some cases, alpine species are resilient under seemingly unfavourable climates. Some examples of these adaptations include low-lying, compact, and slow growing tendencies (Körner, 1995). However, under changing biotic interactions such as the scenario in which new competitors move upslope, they are at a disadvantage (Cavieres et al., 2007; Jägerbrand et al., 2009; Olsen & Klanderud, 2014). Their advantages under harsh conditions are no longer critical and are potentially a hindrance under new biotic and abiotic conditions (Callaway, 2007; Jägerbrand et al., 2009; Klanderud, 2005).

Under these new conditions, arctic-alpine plant species have limited options: move, adapt, or die. Possible solutions could include moving to new habitat "islands" through dispersal (naturally or via assisted migration) (Klanderud & Totland, 2007; Graae et al., 2018); quickly responding and adapting under strong competitive selection (Graae et al.et al., 2018; Klanderud & Totland, 2007; Olsen & Klanderud, 2014); or death and local extirpation. Before we can predict which scenario is most likely, and whether such species should be actively managed via assisted migration, we must first understand their life history and ecological requirements and relationships in potentially threatened habitats (Blonder et al., 2018; Klanderud, 2005).

Alpine plant species are known for their resiliency and hardiness because of their associated climate, glacial history, and geology (Cavieres et al., 2014; Graae et al., 2018). However, there are relatively large variations in what is defined as an alpine ecosystem, which in turn provides an interesting study opportunity of the local and regional systems (Cavieres et al., 2014). A good example of this unique diversity can be seen on the Avalon Peninsula, with the persistence of the arctic-alpine species, *Diapensia lapponica*. Here, we detail the unique life history and ecology of *D. lapponica* on the island of Newfoundland to introduce it as a model species for understanding the unique challenges of arctic-alpine species under ongoing global change.

#### 1.2 Diapensia lapponica life history and ecology

*D. lapponica* is a species of cushion plant within the Diapensiaceae family. Diapensiaceae is a very old taxon associated with arcto-tertiary forest flora. This plant species assemblage, present across the Northern Hemisphere during the late Cretaceous and Paleogene, became disjunct due to extinction resulting from climate change during the Neogene and Quaternary (Deng et al., 2015; Scott & Day, 1983). It presently exists in typical arctic-alpine plant communities with low-lying genera such as *Dryas* spp., *Cassiope* spp., *Arctostaphylos* spp., and *Sibbaldiopsis* spp. Diapensiaceae is composed of five genera (*Diapensia* spp., *Pyxidanthera* spp., *Berneuxia* spp., *Shortia* spp., and *Galax* spp.), 13 species, and one cultivar (Scott & Day, 1983). Most of the species are isolated to eastern Asia, with *D. lapponica* being the only species of its genus to exist in North America (Scott & Day, 1983). There are two subspecies of *D*.

*lapponica: D. lapponica* subsp. *lapponica*, and *D. lapponica* subsp. *obovata*, with distinct geographic distributions (Scott & Day, 1983). *D. lapponica* subsp. *lapponica* is found on the northeastern coast of North America in arctic and alpine regions, Greenland, Scandinavia, Iceland, Scotland, and the western arctic of Russia, while *D. lapponica* subsp. *obovata* is found in Yukon, Alaska, the eastern arctic of Russia, Japan, and Korea (Scott & Day, 1983). The global distribution of *D. lapponica* including both subspecies can be found through databases such as the Global Biodiversity Information Facility (GBIF) which collects data from a number of different sources to provide information on species globally.

Cushion plants are known for their unique dome-shape, adapted to withstand extreme environments that see high winds, extreme cold, and regosol or bare rock. Research has focused on their potential as ecosystem engineers or nurse plants (Badano et al., 2006; Cavieres & Badano, 2009; Cavieres et al., 2014). The cushion (or "duff") retains heat, as well as dust and humidity, sources of nutrients and hydration (Day & Scott, 1981; 1984). Cushion plants can also provide a more hospitable environment for less hardy herbaceous plants, giving them an important role in succession and maintenance of diversity in extreme environments (Badano et al., 2006; Cavieres & Badano, 2009; Cavieres et al., 2014).

*D. lapponica* subsp. *lapponica* (hereinafter *D. lapponica*), is a dwarf, cushion-forming shrub which is adapted for harsh arctic-alpine climates (Day & Scott, 1981). Similar to other cushion plants, its radial growth form can provide a rough estimation of its age (Molau, 1997) *D. lapponica* cushions have three distinct layers. At the base is a main, branching stem, followed by dead stems, and living leaves on the outermost layer (Figure 1.1). The leaves are leathery, small and tightly packed, which aids in temperature regulation. During the summer and early fall, leaves are green. During fall and winter, the anthocyanin concentration in the leaves increases

turning them a dark burgundy (Figure 1.2) (Day & Scott, 1981). Each *D. lapponica* plant has a number of individual flowers that are raised above the cushion on relatively tall peduncles (3-6 cm) (Day & Scott, 1984). The flowers are white with five petals and five stamens (Figure 1.3) (Day & Scott, 1984). Day and Scott (1984) suggest that the tall peduncle raises seed capsules above the snowpack, allowing them to be picked up by the high winds that are often present in harsh environments.



**Figure 1.1.** Adapted cross-section diagram of *D. lapponica* showing the A: inner dead leaf matter; B: densely packed outer living leaves; C: thin branches; D: main stem (Scott and Day, 1981).



**Figure 1.2.** Cross-section of live *D*. *lapponica* cushion (approx. 9 cm diameter) at Hawke Hills Ecological Reserve, NL in September 2019. Scale 1:1.5 (Photo: Baehre, 2019).



**Figure 1.3.** *D. lapponica* flowering (A) alongside an empty peduncle (C) and colour change from green to dark burgundy beginning to occur in leaves (B) during August 2020 at Hawke Hills, NL. Scale 1:1 (Photo: Baehre, 2020).

D. lapponica can be found in a number of locations across Newfoundland and Labrador, notably at Hawke Hills Ecological Reserve (approx. 40 km west of St. John's), atop some of the harshest barrens that exist in the province, and west of Cape Broyle near South West Pond in the Avalon Wilderness Reserve (Day & Scott, 1981). In most localities, D. lapponica generally blooms in June. However, in Newfoundland, there are populations that bloom in August often, including those on the Avalon Peninsula (Day & Scott, 1981). Within a single plant, some flowers will bloom in June and others will bloom in August (Djan-Chékar, 2019). This is unique within D. lapponica populations and although the reasoning behind this phenological variation is unknown, it is suspected that it may be due to more ideal conditions in those areas or predetermined genetically (Day & Scott, 1981; Djan-Chékar, 2019). Plants require a great deal of energy to produce and maintain flowers through the reallocation of resources throughout the year. If conditions are more suitable (slightly warmer, more light availability) for pollination and reproduction, they are more likely to reallocate those resources if feasible in an attempt to support floral development and further establishment (Maia et al., 2013). The Avalon Peninsula D. lapponica populations experience relatively long, warm fall seasons when compared to their arctic experience. South (1983) notes that these hardier arctic-alpine plants existed at approximately 5-10 km from the coast and rapidly decreased in abundance except in the most exposed regions.

#### 1.3 Study Region

#### 1.3.1 Study Sites

The southeastern Maritime Barrens subregion of Newfoundland and Labrador, including the Hawke Hills, is the focus of this research. The first group of our study sites is located along the Hawke Hills (Figure 1.5), which are higher in elevation, and include the Hawke Hills Ecological Reserve, approximately 40 km southwest of St. John's, NL (47.316798, -53.127461).

This is a provincially protected reserve approximately 2.1 km<sup>2</sup> located in the southeastern Barrens Maritime region. The higher elevation points often host arctic-alpine heath because of the plants' ability to establish themselves, where other less hardy plants cannot. The ecological reserve initially became a protected area in 1992 due to the highly specific arctic-alpine plant communities (including *D. lapponica*) and is the most eastern alpine barrens of its kind. The mean annual air temperature for the Hawke Hill Ecological Reserve is approximately 4° C, annual precipitation exceeds 1975 mm with snow being present from December to May, and winds often reach 160 km/hr (Parks & Natural Areas Division, 1992). There is frequently heavy fog and increased precipitation in warmer seasons.

There is little, if any, forest establishment given the harsh conditions. Where trees have established in the lower-lying areas, their growth is highly limited to krummholz, cushion or tuckamore form. The Hawke Hills are home to a collection of rare arctic-alpine species which is unique this far east and south. These species include: lapland pincushion plant (*D. lapponica*), alpine azalea (*Kalmia procumbens*), Highland rush (*Juncus trifidus*), Northern fir moss (*Huperzia selago*), alpine bearberry (*Arctous alpina*), pink crowberry (*Empetrum easmesii*), and several alpine lichen species (*Cetrania nivalis* and *Cetraria cucullate*). Adaptation by these species along with several other heath and tussock forming species have conformed to the extreme winds by forming mats across the area to hold any remaining mineral soil that has not been eroded by slope wash and niveo-aeolian activity (Parks and Natural Areas Division, 1992).

The second group of our two study sites is within the northeastern part of the Avalon Wilderness Reserve overlooking South West Pond (Figure 1.6), approximately 50 km south of St. John's, NL (47.118718, -53.081220). Most of the terrain is rolling plateau where the average elevation is less than 100 m with small ponds and streams are interspersed throughout. There are

scattered outcrops within the interior of the reserve that reach approximately 300 m in elevation which is often where *D. lapponica* and other low-lying vegetation can be found.

The Avalon Wilderness Reserve consists of two ecoregions, the Avalon Forest ecoregion and the southeastern Maritime Barrens sub-ecoregion. Our research focuses on the Maritime Barrens sub-ecoregion, which makes up much of the reserve. The southeastern Maritime Barrens subregion consists of plant communities that are mainly composed of ericaceous dwarf shrubs such as lowbush blueberry (*Vaccinium angustifolium*), bilberry (*Vaccinium uliginosum*), partridgeberry (*Vaccinium vitis-idaea*), and black crowberry (*Empetrum nigrum*) (Parks and Natural Areas Division, 1986). The climate in the Avalon Wilderness Reserve is similar to Hawke Hills, with relatively mild winters, cooler summers, rainfall and fog. The mean annual precipitation is approximately 1390 mm with wind speeds averaging between 25-27.5 km/h (Parks & Natural Areas Division, 1986).

One of the main suggestions by Day & Scott (1978) as to why *D. lapponica* continues to persist on the island of Newfoundland given that it is relatively southern and at low elevations in comparison to its counterparts in the circumpolar and alpine regions is the climatic influences. The Labrador Current creates a cold wall surrounding the island which often results in a moderated but cool oceanic climate. Meteorologically, we see this manifest as fog, high cold winds, rain, and ice – all which arctic-alpine plants such as *D. lapponica* have adapted to thrive in. However, it is predicted that the climate of Newfoundland will change as a result of global climate change over the next 50 years. Across the island, the daily mean temperatures, most notably the winter temperatures, are expected to increase. However, the Avalon Peninsula is likely to be less impacted due to the open water in the vicinity throughout the year (Finnis & Daraio, 2018). During the winter months in regions that experience temperatures around 0

degrees Celsius, it is expected there will be more precipitation falling as rain rather than snow (Finnis & Daraio, 2018). It is also predicted that there will be an increase in growing degree days (GDD), which is the measure of available energy for plant development during the growing season, in all regions across the island (Finnis, 2013; Finnis & Daraio, 2018). More available energy for plant growth during the growing season may mean that plants have increased development, as well as mature earlier. Across the island it is predicted that these increases in GDD will be more significant in the summer (~ 200 additional GDD) and fall (~100 GDD) (Finnis 2013; Finnis & Daraio, 2018).



**Figure 1.4.** Map of the Avalon Peninsula, Newfoundland, Canada with Hawke Hills and Avalon Wilderness Reserve sites. (Map Credit: Ralph Baehre, 2022)



**Figure 1.5.** Map of Hawke Hills study sites surveyed between September 2019 and October 2020 located on the Avalon Peninsula, Newfoundland, Canada. (Map Credit: Ralph Baehre, 2022)



**Figure 1.6.** Map of South West Pond (Avalon Wilderness Reserve) study sites surveyed between September 2019 and October 2020 located on the Avalon Peninsula, Newfoundland, Canada. (Map Credit: Ralph Baehre, 2022)

#### 1.3.2 Geology and soils of the Avalon Peninsula

Based on radiocarbon-dated pollen records, following deglaciation, tundra vegetation established for a short period approximately 10,000 before present (BP) (Macpherson, 1982). This tundra vegetation that was dominated by shrubs began to become overtaken approximately 9300 BP by spruce and balsam fir, and birch in more sheltered areas of the Avalon Peninsula, such as Hawke Hills likely remained relatively devoid of treed vegetation where the soil was not suitable for establishment (MacPherson, 1982). Between 5400 and 3200 BP, the Eastern Avalon Peninsula reached its warmest period with increased precipitation (MacPherson, 1982). Around approximately 5000 BP, this increase in precipitation began to stabilize, but the Avalon Peninsula also began to experience a decrease in temperature which caused the expansion of wetlands in the low points of the terrain (MacPherson, 1995). The exposed high points such as the barrens that neither had the soils nor general topography to become wetlands, may have begun to resemble more closely alpine or tundra landscapes in both climate and vegetation, conditions in which plant species such as *D. lapponica* would have thrived.

The majority of the peninsula is higher than 150m above sea level (a.s.l.) with maximum elevations reaching approximately 330m a.s.l within the Hawke Hills (Catto, 1998). Macpherson (1996) proposed a "downwasting hypothesis" which suggested that the highest points on the Avalon Peninsula, including the Hawke Hills, were deglaciated first prior to the lower-lying regions. These higher elevation points are now frequently home to several arctic-alpine flora, moss, and lichen species, such as *D. lapponica, Kalmia procumbens* and *Racomitrium lanuginosum* that are more adapted to these exposed conditions.

The rocks found in the Hawke Hills Ecological Reserve and parts of the Avalon Wilderness Reserve are composed of granite from the Holyrood intrusive suite (Catto, 2020).

This granitic parent material is highly resistant to environmental modification with very little topsoil and is generally acidic, creating a harsh environment for potential colonizing vegetation (Catto, 2020). Randomly deposited glacial erratics and outcrops are numerous in the barrens. In higher elevation areas that are exposed, sometimes due to anthropogenic disturbance, frost action dominates the landscape (Catto, 2020; Taylor 1994). From the 17th to 19th centuries in some coastal communities, land clearing was prevalent to allow for livestock grazing (Catto, 2020; Henderson 1972). This, paired with extreme wind erosion in the Hawke Hills causes reduced snow cover, intermittent vegetation cover, and a reduced humus layer making these regions prone to a strong freeze-thaw process resulting in patterned ground (Protected Areas Association of Newfoundland and Labrador, 2008), the natural sorting and distribution of sediment and frostshattered bedrock as a result of intense periglacial activity. This regular disturbance limits the establishment of most species but provides a natural successional process for the local flora which are suited to this type of extreme climate (Protected Areas Association of Newfoundland and Labrador, 2008). Human interactions with the barrens landscape can also influence the persistence of stone circles in that the disturbance of vegetation is correlated with an increased degree of patterned ground development (Taylor, 1994).

## 1.3.3 Protected Areas and Human Activities

A large portion of our study sites where *D. lapponica* is found on the Avalon Peninsula are within provincially protected areas which the province of Newfoundland and Labrador (as adapted from the International Union for Conservation of Nature) defines as, "An area of land and/or sea especially dedicated to the protection and maintenance of biological diversity, and of natural and associated cultural resources, and managed through legal or other effective means" (Natural Areas Program, n.d.). These protected areas come in many different forms including

provincial parks, wildlife reserves, wildlife parks, special management areas, and as in the case of our research, ecological and wilderness reserves. The latter two are protected under the *Wilderness and Ecological Reserves Act* (1980) and associated regulations. According to s. 24 of the *Wilderness and Ecological Reserves Act* (1980), there are several rules and regulations in place including the strict prohibition of: destruction or removal of plants, animals, and fossils; introduction of plants or animals; forestry and mining; powerline development; agriculture; new roads, tracks, or other construction; and driving any type of vehicle. As well, hiking and research should be minimally destructive as possible.

The first of our study regions is located along the Hawke Hills (Figure 1.5). The Hawke Hills Ecological Reserve was established in 1992 to protect the rare arctic-alpine plant and lichen species (e.g., *D. lapponica, Arctous alpina*, and *Kalmia procumbens*) that are present (Parks and Natural Areas Division, 1992). According to s. 5 of the *Wilderness and Ecological Reserves Act* (1980), ecological reserves are areas that are representative of a unique ecosystem, species, or natural phenomena. They are meant to provide opportunity for habitat or preservation of rare or endangered species which may include the preservation of unique geological, botanical, zoological or geographical characteristics, and allow for study, research, and educational purposes regarding the natural environment. Although there are limitations to development and resource extraction in the Hawke Hills Ecological Reserve, some personally-noted frequent human activity that exists includes; the use of all-terrain vehicles (ATV) along the trail to reach hunting grounds further inland outside of the reserve, hiking by sightseers and researchers along the trail and among the vegetation, and the development of a power transmission line.

The second of our two study regions is within the northeastern part of the Avalon Wilderness Reserve overlooking South West Pond (Figure 1.6). This 1070 km<sup>2</sup> provincially

protected wilderness reserve was established in 1964 to preserve a number of plant and animal species and foster an "untouched" region of the Avalon Peninsula (Parks and Natural Areas Division, 1986). According to s. 4 of the *Wilderness and Ecological Reserves Act* (1980), wilderness reserves are areas that are preserved to provide continued existence of large, undisturbed natural environments for individuals to hunt, fish, travel, and appreciate, as well as, allowing for flora and fauna to interact relatively unhindered. Although there are limitations to development and resource extraction in the Avalon Wilderness Reserve, some personally-noted frequent human activity includes hunting, fishing, camping, and hiking.

## **1.4 Previous Research and Thesis Objectives**

The *D. lapponica* populations on the island of Newfoundland have been the focus of botanical and mainly taxonomic research in the past. As a species in general, much of the details and information were contributed by Robin Day & Peter J. Scott during the late 1970s and 1980s. In general, it seems that the specialization of this species makes it interesting from a natural history perspective but perhaps, reaches less of a broad scientific (or non-scientific) community.

When it comes to the species-specific literature, this is reduced even less when looking for location specific material. Day, Scott, Rouleau, Hermanutz, Danman, Boland, and Maunder, associated with the Newfoundland and Labrador government, Memorial University, or citizen science initiatives have contributed to information on *D. lapponica* and other highly specialized species through the Rare Plant Project and Labrador Straits Plant Project (Djan-Chékar & Hanel, 2004). However, no published research has quantified the specific habitat and ecological requirements of *D. lapponica*, and no research has been done in the context of contemporary climate change.

Throughout this thesis, we will fill in the research gaps to begin to quantify the specific life history requirements and habitat, and ecology of *D. lapponica* in the unique communities found on the Avalon Peninsula, to better understand how they may be threatened, and managed, in the future. Our research objectives include and take a hierarchical approach from small to large scale:

- Quantifying the role *D. lapponica* plays in moderating their own microclimate;
- Characterizing the arctic-alpine plant communities on the Avalon Peninsula on the island of Newfoundland;
- Improving understanding of *D. lapponica*'s habitat requirements through observations of microtopography and ground cover; and
- Understanding how local *D. lapponica* communities compare to those across eastern North America

#### **1.5 Thesis organization**

In this chapter, we have summarized the context for the scope of our research and addressed gaps in knowledge. We discussed the life history traits of *D. lapponica* on the Avalon Peninsula and in its general distribution as a species. We also described the study sites and the environmental characteristics (e.g.,, geology, climate, glacial history) of those sites and the Avalon Peninsula that are relevant to the persistence of *D. lapponica*. Following this, we briefly describe the protected areas of Newfoundland and Labrador and their importance in the protection of *D. lapponica*. Chapter 2 is prepared as a manuscript and summarizes the primary research of this thesis. Here we describe our methods, analysis and interpretation of the empirical data collected to discuss how environmental characteristics including microclimate,

microtopography, and ground cover, as well as, biological characteristics such as plant community composition and vascular plant species richness, influences the populations of *D*. *lapponica* on the Avalon Peninsula. In Chapter 3, we reflect on those findings and connect them to management and conservation of *D. lapponica*.

### **1.6 References**

- Badano, E.I., Jones, C.G., Cavieres, L.A., & Wright, J.P. (2006). Assessing impacts of ecosystem engineers on community organization: a general approach illustrated by effects of a high-Andean cushion plant. *Oikos*, *115*(2), 369-385.
- Blonder, B., Kapas, R. E., Dalton, R. M., Graae, B. J., Heiling, J. M., & Opedal, Ø. H. (2018). Microenvironment and functional-trait context dependence predict alpine plant community dynamics. *Journal of Ecology*, 106(4), 1323-1337.
- Callaway, R. M. (2007). *Positive interactions and interdependence in plant communities*. Springer Science & Business Media.
- Catto, N. R. (1998). The pattern of glaciation on the Avalon Peninsula of Newfoundland. *Géographie Physique et Quaternaire*, 52(1), 23–45.
- Catto, N. R. (2020). The Avalon of Newfoundland: Geomorphology, People and Landscape. In *World Geomorphological Landscapes* (pp. 333–367).
- Cavieres, L. A., Badano, E.I., Sierra-Almeida, A., & Molina-Montenegro, M. A. (2007). Microclimatic modifications of cushion plants and their consequences for seedling survival of native and non-native herbaceous species in the high Andes of central Chile. *Arctic, Antarctic, and Alpine Research*, 39(2), 229-236.
- Cavieres, L. A., & Badano, E. I. (2009). Do facilitative interactions increase species richness at the entire community level? *Journal of Ecology*, 97(6), 1181–1191.
- Cavieres, L. A., Brooker, R. W., Butterfield, B. J., Cook, B. J., Kikvidze, Z., Lortie, C. J., ... & Callaway, R. M. (2014). Facilitative plant interactions and climate simultaneously drive alpine plant diversity. *Ecology letters*, 17(2), 193-202.
- Day, R. T., & Scott, P. J. (1981). Autecological aspects of *Diapensia lapponica* L. in Newfoundland. *Rhodora*, 83(833), 101-109.
- Day, R. T. & Scott, P. J. (1984). The biology of *Diapensia lapponica* in Newfoundland. *Canadian Field-Naturalist*, *98*, 425-439.

- Djan-Chékar, N. (2019). Personal Communication. Natural History Collections Manager at The Rooms Provincial Museum.
- Djan-Chékar, N. & Hanel, C. (2004). The Newfoundland Rare Plant Project. https://www.gov.nl.ca/ffa/files/wildlife-biodiversity-rare-plant-project-nl-rare-plant-reportapril2004.pdf
- Finnis, J. (2013) Projected impacts of climate change for the province of Newfoundland and Labrador. Technical report submitted to: The Office of Climate Change, Energy Efficiency & Emissions Trading. St. John's: Provincial Govt. of Newfoundland and Labrador.
- Finnis, J., & Daraio, J. (2018) Projected impacts of climate change for the province of Newfoundland and Labrador: 2018 update. Technical report submitted to: The Office of Climate Change, Energy Efficiency & Emissions Trading. St. John's: Provincial Govt. of Newfoundland and Labrador.
- Graae, B. J., Vandvik, V., Armbruster, W. S., Eiserhardt, W. L., Svenning, J. C., Hylander, K., ... & Lenoir, J. (2018). Stay or go-how topographic complexity influences alpine plant population and community responses to climate change. *Perspectives in Plant Ecology*, *Evolution and Systematics*, 30, 41-50.
- Jägerbrand, A. K., Alatalo, J. M., Chrimes, D., & Molau, U. (2009). Plant community responses to 5 years of simulated climate change in meadow and heath ecosystems at a subarcticalpine site. *Oecologia*, 161(3), 601-610.
- Klanderud, K. (2005). Climate change effects on species interactions in an alpine plant community. *Journal of Ecology*, 93(1), 127-137.
- Klanderud, K., & Totland, Ø. (2007). The relative role of dispersal and local interactions for alpine plant community diversity under simulated climate warming. *Oikos*, *116*(8), 1279-1288.
- Körner, C. H. (1995). Alpine plant diversity: a global survey and functional interpretations. In *Arctic and alpine biodiversity: patterns, causes and ecosystem consequences* (pp. 45-62). Springer, Berlin, Heidelberg.
- MacPherson, J.B. (1982). Postglacial vegetational history of the eastern Avalon Peninsula, Newfoundland, and holocene climatic change along the eastern Canadian seaboard. *Géographie Physique et Quaternaire*, *36*(1-2), 175-196.
- MacPherson, J.B. (1995). A 6 ka BP reconstruction for the island of Newfoundland from a synthesis of holocene lake-sediment pollen records. *Géographie physique et Quaternaire*, 49(1), 163-182.

- MacPherson, J.B. (1996). Delayed deglaciation by downwasting of the northeast Avalon Peninsula, Newfoundland: an application of the early postglacial pollen record. *Géographie Physique et Quaternaire*, 50(2), 201–220.
- Maia, F. R., Malucelli, T. S., & Varassin, I.G. (2013). Ecological factors affecting the fruiting success of a *Tibouchina trichopoda* (DC.) Baill. (*Melastomataceae*) flower. *Acta Botanica Brasilica*, 27, 142-146.
- Molau, U. (1997). Age-related growth and reproduction in *Diapensia lapponica*, an arctic-alpine cushion plant. *Nordic Journal of Botany*, *17*(3), 225–234.
- Natural Areas Program. (n.d.). *Protected Areas in Newfoundland and Labrador*. https://www.gov.nl.ca/ecc/apa/
- Kudo, G., Kawai, Y., Amagai, Y., & Winkler, D. E. (2017). Degradation and recovery of an alpine plant community: experimental removal of an encroaching dwarf bamboo. *Alpine botany*, 127(1), 75-83.
- Olsen, S. L., & Klanderud, K. (2014). Biotic interactions limit species richness in an alpine plant community, especially under experimental warming. *Oikos*, *123*(1), 71-78.
- Parks and Natural Areas Division. (1986). Avalon Wilderness Reserve Management Plan. Department of Environment and Conservation – Government of Newfoundland and Labrador, 1-32.
- Parks and Natural Areas Division. (1992). Hawke Hills Ecological Reserve Management Plan. Department of Environment and Conservation – Government of Newfoundland and Labrador, 1-19.
- Protected Areas Association of Newfoundland and Labrador (PAANL). (2008). Maritime barrens: Southeastern barrens subregion. Newfoundland and Labrador Ecoregion Brochures, (36), 4.
- Scott, P. J., & Day, R. T. (1983). Diapensiaceae: a review of the taxonomy. Taxon, 417-423.
- South, R. (1983). *Biogeography and Ecology of the Island of Newfoundland* (Vol. 48). Springer Science & Business Media.
- Taylor, C.R. (1994). *The formation of soil frost related patterns along the Hawke Hills*. (MSc thesis, Department of Geography, Memorial University of Newfoundland, 53 pp).
- Wilderness and Ecological Reserves Act, Royal Statutes of Newfoundland and Labrador (1980, c. W-9). Retrieved from the Office of the Legislative Counsel Newfoundland and Labrador website: https://www.assembly.nl.ca/legislation/sr/statutes/w09.htm

#### Chapter 2: Hierarchies of Habitat: Diapensia lapponica on the Avalon Peninsula

#### 2.1 Introduction

Global drivers of change are having cumulative effects on plant communities. Climate change has driven the expansion, retraction, and shift of species ranges, in some cases significantly altering historical compositions of plant communities and biotic interactions (Hobbs et al., 2013). Extremes in temperatures, precipitation, and other weather phenomena can create or ease limitations to growth (Larcher et al., 2010). Land use changes such as deforestation or construction of roads or powerlines can interact with climate change and contribute to the redistribution of species through loss of appropriate habitat (Guo et al., 2018). In response to these cumulative stressors, a species can adapt to the new conditions, move by dispersal to more suitable areas (depending on limitations in terms of their life history), or go locally or globally extinct (Graae et al., 2018).

Certain plant communities have very specific and geographically constrained habitat requirements that may be especially threatened because they have no alternative location to shift to. Small populations with low fecundity are less likely to adapt in time to respond to stressors. Several examples of this have been documented on global and local scales for arctic-alpine communities. Alexander et al. (2015) found that high alpine plant communities may be increasingly threatened in the Swiss Alps, as novel competitors encroach from lower elevations. Another example of geographically constrained species can be seen in Fennoscandia, Northern Europe where range contraction of arctic-alpine species, *Ranunculus galcialis*, and arctic species, *Draba nivalis*, are projected to reach endangered (loss of  $\geq$  50%) or critically endangered (loss of  $\geq$  80%) under predicted future climate change (Niksanen et al., 2019). The inability of species to

move poleward may result in range size contraction which could drastically reduce the diversity of high-alpine communities (Niksanen et al., 2019).

The island of Newfoundland is home to a number of unique plant communities, including arctic-alpine plant assemblages restricted to exposed barrens (Damman, 1976; South, 1983). These plant communities are composed of species characterized by slow annual growth (less than 5mm/year), low-lying habit, and limited reproduction and dispersal mechanisms, which are often not well understood (Day & Scott, 1984). Many of these species have sturdy main stems and thick leaf cuticles. Both vascular plants (e.g., K. procumbens) and mosses are densely packed (e.g., acrocarpous moss) with fruticose lichens interspersed or crustose and small-stature foliose lichens found on the rocky ground. These communities are distinct because they are controlled by harsh environmental conditions and disturbed substrate in coastal environments. They can withstand extreme wind, cooler summer temperatures, little insulation from snow during winter months, and marine salt spray throughout the year (Damman, 1976; Day & Scott, 1981). As well, they establish and survive in areas with very little topsoil, marked by substantial freeze-thaw or natural disturbance to form mixed-texture gravel substrates for establishment (Sutton et al., 2006). Additionally, some species are endemic to areas with very specific substrates (e.g., limestone barrens) (Driscoll, 2006).

These rugged but highly specialized arctic-alpine plant communities are often directly threatened by human disturbance. Recreational land use, such as removal or compaction of substrate by all-terrain vehicles (ATVs), may result in a more uniform collection of substrate gravel while simultaneously damaging the plants themselves (Robinson & Hermanutz, 2015). Altering the substrate texture affects the ability of substrates to hold water and nutrients in already relatively resource-deficient locations as well as potentially changing the dimensions of the substrate that results from natural freeze-thaw disturbances that are vital for arctic-alpine species seed establishment (Driscoll, 2006; Kevan et al., 1995; Robinson & Hermanutz, 2015; Sutton et al., 2006). Indirectly, human-driven climate change may provide challenges for these slow-growing, weak competitors by providing more hospitable habitat for faster-growing competitors to encroach as seen in other systems (Alexander et al., 2015). Slow-growing, weak competitive species have adapted to survive in these challenging conditions while others cannot, but as conditions change these adaptations become disadvantageous. On the Avalon Peninsula, ruderal or wind-dispersed species like *Solidago* spp. may be primed to colonize these habitats by creeping in from the sides, eventually growing in overtop of low-lying plants like *D. lapponica* and *K. procumbens* (Sullivan, 2020).

A particularly unique, defining species in arctic-alpine communities is *Diapensia lapponica*. It can be found in Greenland, Scandinavia, Iceland, Scotland, and the western arctic of Russia, as well as the northeastern coast of North America in arctic and alpine regions from New England, USA to Nunavut, Canada (Scott & Day, 1983). *D. lapponica* is a slow-growing species of cushion plant that is highly adapted to cold climates. These adaptations include frost resistance, and the ability to absorb high amounts of solar radiation through its densely packed leathery leaves, while retaining moisture and dust in its inner matrix of dead leaf material (Chen et al., 2017; Day & Scott, 1984; Molau, 1996). It is often found in windswept arctic-alpine or tundra environments, and forms relatively sparse communities with other woody and ericaceous species, sedges, mosses, and lichens (Bliss, 1963; Day & Scott, 1981; Molau, 1996). Cushion plants play an important role in harsh environments as nurse plants in that they can provide a more hospitable environment for less hardy forbs and aid in the process of succession as well as the maintenance of biodiversity and in turn, ecosystem resiliency (Badano et al., 2006; Cavieres

& Badano, 2009; Cavieres et al., 2014). Understanding the way *D. lapponica* functions in other plant communities regionally and globally helps to inform the drivers of arctic-alpine plant community assemblage locally.

Arctic-alpine plant communities may be under threat due to land use changes and encroachment by other types of plant communities, such as boreal forest or more dense heath. On the island of Newfoundland, arctic-alpine communities often characterized by *D. lapponica* are particularly unique and should receive continued attention for conservation and monitoring. The objective of our study took a hierarchical approach and was to i) quantify the role *D. lapponica* plays in moderating their own microclimate; ii) characterize the arctic-alpine plant communities on the Avalon Peninsula on the island of Newfoundland; iii) improve our understanding of *D. lapponica*'s habitat requirements through observations of microtopography and ground cover; and iv) understand how local *D. lapponica* communities compare to those regionally across eastern North America.

#### 2.2 Methods

#### 2.2.1 Study area

Our study occurred on the eastern part of the Avalon Peninsula on the island of Newfoundland, Canada, on the traditional lands of the Beothuk people. Here, the Southeastern Maritime Barrens subregion provides pockets of foggy, windswept, higher elevation habitat that mimic an arctic-alpine environment amidst valleys of boreal forest (Protected Areas Association of Newfoundland and Labrador, 2008; South, 1983).

Within this subregion, we sampled from three different locations in the Hawke Hills and two locations in the Avalon Wilderness Reserve located near South West Pond (**Figure 1.4**). The Hawke Hills are dominated by exposed rock, high winds up to 120 km/h, and dense fog. These
hills represent some of the highest elevations on the Avalon Peninsula. Our sites were between 250 and 300 m a.s.l. and are approximately 15 kmfrom the ocean. Within the Hawke Hills, there is a small provincially protected area, designated due to its ecological significance for its population of arctic-alpine plants, mosses, and lichens.

The Avalon Wilderness Reserve is also a provincially protected area. This area is dominated by wetlands, boreal forest, and glacially-scoured bedrock, the latter hosting *D*. *lapponica*. The elevations at our two sample sites are between 200 and 250 m a.s.l. and the distance from the ocean is approximately 17 km.

#### 2.2.2 *Field methods*

# 2.2.2.1 Community composition of the Avalon Peninsula

To evaluate the community composition associated with *D. lapponica*, we assessed the vegetation community assemblage where *D. lapponica* persisted at each site by setting up five-50 m-transects (20 m apart). These transects were laid out to capture as much of the site variation as we could across the barrens and best represent the overall habitat of *D. lapponica*. We estimated percent cover of plant species or vegetation group (for mosses and lichens) within  $1m^2$ -quadrats beginning at 0m and ending at 40 m (5 quadrats x 5 transects = 25 quadrats per site) at all five sites (*Figure 2. 1*). Mosses were grouped into: acrocarpous and pleurocarpous, and lichens were grouped into fruticose, crustose, and foliose. Given that the percent cover estimation is relatively subjective, these observations were completed by the same individual for all quadrats at each of the sites. The geographic coordinates of the start and end point of each transect was marked using a GPS.



**Figure 2. 1.** Study design for assessing plant community composition associated with *D*. *lapponica* (blue) and microtopography features (red) at three sites in the Hawke Hills and two sites in the Avalon Wilderness Reserve.

## 2.2.2.2 Microtopgraphy

To identify links between microtopographic features and *D. lapponica* occurrence, we quantified the microtopographic features occurring across each site. Using a 50m transect laid at 90° across the plant community composition transects, we recorded the microtopographic feature present and the length on the transect where the feature occurred (*Figure 2. 1*). Placing the microtopography transect at 90° across the plant community composition transects was done to further capture as much site variation as possible. Microtopographic features were defined subjectively, relative to flat rock features in the study sites (Figure 2. 2). The lowest feature that we defined was a "crevice", which was observed to be below the level of flat rock. Above flat rock or "flat", the next highest feature defined was a "mat", which was raised slightly above "flat" (by eye, approximately 2-5 cm) (Figure 2. 3). The highest feature we defined was a

"mound", which was well above the level of flat rock and mat (by eye, approximately 6-30 cm) (Figure 2. 3). We also noted what type of ground cover was associated with each microtopographic feature observed along the transect, which included the categories: vegetation, covered rock, and rock.



Figure 2. 2. Microtopography features in relation to one another on the Avalon Peninsula, island of Newfoundland.



**Figure 2. 3.** Demonstration of the four microtopography features; A. Crevice, B. Flat, C. Mat, D. Mound, observed on the Avalon Peninsula during field surveys in Fall 2020.

# 2.2.2.3 Microclimate

To better understand the climate that *D. lapponica* and its surrounding plant communities experience, as well as the potential microclimate associated with the cushion plant, we placed five pairs of temperature loggers (Maxim Integrated, iButton Thermochron, DS1921G-F5#) randomly at each of our five sites. To directly quantify the microclimate within the cushion relative to exposed microsites, one logger of each pair was placed below the protective cover of the *D. lapponica* cushion but was not buried in the gravel substrate, while the other was placed below ground (approximately 3 cm) under vegetation or bare ground. The latter temperature logger was placed below the ground slightly to first, prevent the metal from absorbing additional heat due to its material, resulting in inaccuracy, and second, prevent them from being scoured away by the wind. The pair of loggers were placed within 10 cm of one another (Figure 2. 4). Loggers recorded temperature (°C) every 4 hours from Fall 2019 to late Summer 2020.



**Figure 2. 4.** iButton Thermochron temperature loggers inserted below *D. lapponica* cushion (top left) and below ground cover approximately 2.5-3 cm (bottom right).

## 2.2.2.4 Community Composition for eastern North America

To compare plant communities associated with *D. lapponica* across Eastern North America with the Avalon Peninsula assemblages, we first collated plant occurrence data from a variety of sources. We contacted arctic-alpine botany experts from Canada and the United States, including Paul Sokoloff (Canadian Museum of Nature), Zoe Panchen (University of British Columbia), Sergei Ponomarenko (Canadian Museum of Nature), Anna Crofts (Université de Sherbrooke and formerly Memorial University), and Georgia Murray (Appalachian Mountain Club). Each expert provided community composition data where *D. lapponica* was present in their study sites (S. Ponomarenko, Z. Panchen, and A. Crofts) or directed us to the online herbaria or databases containing *D. lapponica* records.

To obtain community composition data for New Hampshire, New York, Vermont, and Maine, we used iNaturalist observation photographs (many from the Northeast Alpine Flower Watch Project, <u>https://www.inaturalist.org/projects/northeast-alpine-flower-watch</u>) of *D. lapponica* to identify the surrounding vegetation community. For each State, our objective was to process 25 photographs if they were available.. For the Canadian Arctic Archipelago, we accessed the Canadian Museum of Nature online herbarium collections on the Global Biodiversity Information Facility to compile individual observations of *D. lapponica* and their associated plant species in a number of locations across Nunavut included observations from Queen Maud Bird Sanctuary, Beverly Lake, Baffin Island, and Flaherty Island. The area of Nunavut is quite large and these different regions were dispersed widely however, we were limited by the availability of the collections data. For all the above-mentioned observations, we noted the latitude, longitude, and elevation if available.

## 2.2.3 Statistical analyses

# 2.2.3.1 Community Composition of the Avalon Peninsula

All statistical analyses were conducted in R (R Core Team, 2021 using RStudio version 4.1.2. To characterize the community composition of our study sites on the Avalon Peninsula, we used non-metric multidimensional scaling (NMDS; *vegan* package version 2.5.7. (Oksanen et al., 2020), using our percent cover estimates of ground cover (including vascular plant species, mosses, lichens, and rock) for all surveyed plots. To reduce the overrepresentation of rare species, we removed species that occurred in  $\leq$ 10% of the 125 quadrats sampled. Our final NMDS was run using Bray-Curtis coefficients as measures of dissimilarity. The best solutions were reached under three dimensions after approximately 200 iterations. We then created two convex hulls representing groupings of community composition dissimilarity for communities where *D. lapponica* was present and absent.

Our NMDS showed that *D. lapponica* tended to be associated with low-growing, woody vascular plant species and rock cover. This observation and the slow growing tendencies and weak competitive abilities of *D. lapponica*, led us to assess whether vascular plant species richness and rock cover were associated with the presence and extent of *D. lapponica*. The vascular richness encapsulated all of the vascular plant species found in each quadrat, not only the dominant ground cover species. To do this, we applied a two-step approach using generalized linear mixed models (GLMM) and the *glmmTMB* package version 1.1.2.3. (Brooks et al., 2017; Zuur et al., 2009).

Both models used included vascular plant species richness, rock percent cover, and the interactive effects of the two as main effects, and the random effect of plot nested within sites. For our two-step approach, we first used a GLMM with a binomial distribution to determine

whether the presence or absence of *D. lapponica* was associated with our predictor variables. Where *D. lapponica* was present, we then used a GLMM with a beta distribution with the percent cover, i.e., extent, of *D. lapponica* as the response variable.

## 2.2.3.2 Community Composition for eastern North America

To compare the composition of communities across *D. lapponica*'s Eastern North American range, we again used an NMDS approach in *vegan* (Oksanen et al., 2020), this time including the presence-absence of plant species and other ground cover in communities where *D. lapponica* occurred. The best solutions were reached under three dimensions after approximately 200 iterations. we then created seven convex hulls representing groupings of community composition dissimilarity for each of the regions (Avalon Peninsula, Maine, New Hampshire, New York, Northern Peninsula, Nunavut, and Vermont) to assess the variation in community composition in communities where *D. lapponica* is found across Eastern North America. To assess the role of potential environmental gradients associated with community composition, we overlaid latitude and elevation vectors on our final NMDS plot.

## 2.3 Results

# 2.3.1 Cushion-level characteristics

## 2.3.1.1 Microclimate

The internal cushion temperatures suggest that *D. lapponica* provides a moderating effect on maximum and minimum temperatures at the Hawke Hills and South West Pond (Avalon Wilderness Reserve) sites. Although, one temperature logger from each pair was under a small amount of soil, we still see the maximums and minimums. While the average temperature recorded for internal *D. lapponica* cushion and exposed ground are similar (Figure 2. 5 & Figure 2. 6), the maximum and minimum internal cushion temperatures were less extreme than those

recorded on exposed ground (Figure 2. 7 & Figure 2. 8).



**Figure 2. 5.** Average temperatures (°C) of internal cushion (red) and exposed (blue) ground at Hawke Hill Ecological Reserve (n=15) and South West Pond (Avalon Wilderness Reserve) (n=10) sites between November 2019 and August 2020.



**Figure 2. 6.** Average temperatures (°C) of internal cushion and exposed ground between November 2019 and August 2020.



**Figure 2. 7**. Maximum temperatures (°C) of internal cushion and exposed ground between November 2019 and August 2020.



**Figure 2. 8.** Minimum temperatures (°C) of internal cushion and exposed ground between November 2019 and August 2020.

2.3.2 Community-level characteristics

#### **2.3.2.1** Community composition and population characteristics on the Avalon Peninsula

*D. lapponica* in Hawke Hills and South West Pond in the Avalon Wilderness Reserve was associated with a suite of arctic/alpine species (Table A. 1) such as *Vaccinium uliginosum* and *Kalmia procumbens*, as well as species that prefer drier environments such as grasses and *Sibbaldiopsis tridentata*. It was not associated with moisture-loving species such as *Chamaedaphne calyculata*, *Kalmia polifolia*, and *Andromeda polifolia* (Figure 2. 9).



**Figure 2. 9.** Non-metric multidimensional scaling (NMDS) plot describing the community composition of surveyed sites at Hawke Hill Ecological Reserve and South West Pond (Avalon Wilderness Reserve) on the Avalon Peninsula of Newfoundland. The turquoise and green convex hulls indicate the clusters of communities where *D. lapponica* is most commonly present or absent, respectively. Each point represents a ground cover community observed in a 1m<sup>2</sup> quadrat. NMDS diagrams show similarities (or dissimilarities) of communities based on the distance

between points. The farther apart the points are, the more dissimilar the communities are and vice versa.

The interaction between ground cover and vascular richness was positively associated with both the presence and cover of *D. lapponica* (Table 2. 1, Table 2. 2). As rock cover decreases to less than 50%, the cover of *D. lapponica* decreases. Locations with more than 50% rock cover have higher coverage of *D. lapponica* (Figure 2. 10). In locations with high vascular richness and less rock cover, there is less cover of *D. lapponica* (Figure 2. 10). In locations with more than 50% rock cover, increases in vascular richness do not influence the cover of *D. lapponica* (Figure 2. 10). Although we observed increase in *D. lapponica* with vascular plant species richness when rock cover was more than 50% (Figure 2. 10), this relationship was statistically non-significant (p = 0.0907 and 0.1326, Table 2. 1)

**Table 2. 1.** Parameter estimates with standard errors (SE) for generalized linear mixed models of presence of *D. lapponica* (observed within 1m2 quadrats; Binomial distribution) as a function of vascular richness and percent cover of rock (observed within 1 m2 quadrats). This model included site and plot as nested random effects. Significant ( $\alpha = 0.05$ ) covariate estimates are bolded.

	Estimate	Standard Error	Z	р
(Intercept)	0.5437	1.9622	0.272	0.7853
Vascular Richness	-0.3202	0.2129	-1.504	0.1326
% Rock	-4.8788	2.8842	-1.692	0.0907
Vascular Richness: % Rock	0.6960	0.3491	1.993	0.0462

**Table 2. 2.** Parameter estimates with standard errors (SE) for generalized linear mixed models of percent cover of *D. lapponica* (observed within 1 m<sup>2</sup> quadrats; Beta regression analysis) as a function of vascular richness and percent cover of rock (observed within  $1 \text{ m}^2$  quadrats). This model included site and plot as nested random effects.

	Estimate	Standard Error	Z	р
(Intercept)	0.01621	1.59049	0.010	0.992
Vascular Richness	-0.04922	0.17686	-0.278	0.781
% Rock	-1.95983	2.43669	-0.804	0.421
Vascular Richness: % Rock	0.20736	2.9425	0.705	0.481



**Figure 2. 10.** Plot demonstrating the influence of the interaction between the number of vascular plant species and percent rock cover on percent cover of *D. lapponica*. Light blue shaded area represents the standard error.

#### 2.3.2.2 Microtopography

Individual study sites and microtopography features were compared (Figure 2. 11) initially to determine if there was a relationship between microtopography features and the number of *D. lapponica* present. There was a number of similarities between sites, so when we combined the data for the Avalon Peninsula, we found that a higher proportion (%) of mats and mounds had *D. lapponica* than flat or crevices, but no specific trend relating to rock, vegetation, or covered rock was identified (Figure 2. 12). We also found that mounds and mats were the greatest proportions (%) of the sampled microtopographic landscape while crevices were the lowest proportion of the landscape (**Error! Reference source not found.**). Mounds have the greatest of proportion of *D. lapponica* (*Figure 2. 13*).



**Figure 2. 11.** Number of *D. lapponica* individuals observed across four microtopographical features (crevice, flat, mat, mound) at two sites near South West Pond (Avalon Wilderness Reserve) and three sites in the Hawke Hills on the Avalon Peninsula, NL in Fall 2020.



**Figure 2. 12**. Proportion (%) of *D. lapponica* observed on three types of ground cover (rock, vegetation, or vegetation and rock mix) across four microtopographical features (crevice, flat, mat, mound) on the Avalon Peninsula, NL between Fall 2020.



**Figure 2. 13**. Proportion (%) of *D. lapponica* across four microtopographical features (crevice, flat, mat, mound) and proportion (%) of each of the four microtopographical features across the microtopographical landscape on the Avalon Peninsula, NL in Fall 2020.

#### 2.3.3 *Regional-level characteristics*

## 2.3.3.1 Community composition of eastern North America

The plant communities associated with *D. lapponica* across Eastern North America follow a latitudinal gradient (represented by the blue environmental vector, Figure 2. 14), forming two main groupings. Four regions within Nunavut, including Queen Maud Bird Sanctuary being the highest latitude followed by Beverly Lake, Baffin Island, and Flaherty Island as the lowest latitude, compose the northern grouping while New Hampshire, New York, Maine, and Vermont compose the southern grouping. The Northern and Avalon Peninsula groups are more centrally located with respect to the other groupings, corresponding with their latitude in relation to the other locations represented. The northern grouping, which experiences a limited growing season with sub-arctic to arctic climates, is dominated by low-stature woody shrubs such as *Betula* spp., *Salix* spp., and *Alnus alnobetula* as well as low-stature ericaceous shrubs such as *Cassiope tetragona* and *Rhododendron tomentosum*, and sedges. The southern grouping, which experiences a longer growing season and relatively temperate climates, is dominated by a mix of hardier herbaceous plant species such as *Sibbaldiopsis tridentata*, *Solidago* spp., and grasses, as well as a greater variety of low-stature ericaceous shrubs such as *Vaccinium spp., Rhododendron* spp., and *Kalmia* spp.. The southern group is generally associated with higher elevations as denoted by the blue arrow vector (**Error! Reference source not found.**). The Northern and Avalon Peninsulas of Newfoundland are dominated by a mixture of arctic and alpine species found in the northern and southern grouping such as *Arctous* spp., *S. tridentata, K. procumbens*, and *A. alnobetula*.



**Figure 2. 14.** NMDS of composition for communities where *D. lapponica* is present in other Eastern North American locations. Ordination diagrams show similarities (or dissimilarities) of communities based on the distance between points. The further apart the points are, the more dissimilar the communities are and vice versa. Overlain blue vectors represent environmental factors such as latitude and elevation (included in this figure) that may drive the plant communities where the directional arrow trends towards.

# 2.4 Discussion

We have presented evidence that the populations of arctic-alpine cushion plant, *D. lapponica*, on the Avalon Peninsula region of Newfoundland create microhabitats for less hardy plant species within their cushion through the amelioration of temperature. These populations were found to require a specific ideal habitat, including an extent of bare rock and an area with additional vascular plant species, but not an overabundance of either. Within this ideal habitat, we also found that *D. lapponica* is more commonly observed on higher microtopography features flanked by lower lying areas that have greater resource availability (e.g., soil, moisture, protection from wind). As *D. lapponica* is an arctic-alpine plant, the regions which have suitable habitat vary. However, plant communities associated with *D. lapponica*'s range follow a latitudinal and elevational gradient across Eastern North America. The next section further discusses these findings.

## 2.4.1 Cushion-scale characteristics

*D. lapponica* populations on the Avalon Peninsula exhibit a moderating effect on temperature within their cushion structure, characteristic of cushion plants in arctic-alpine environments. This moderating effect is likely due to the inner dead leaf material that acts as a sieve to trap dust and moisture (Cavieres et al., 1998; Day & Scott, 1984), establishing a microclimate that varies from the external environment (Arroyo et al., 2003; Cavieres et al., 2007; Day & Scott, 1981). Cushion plants, including *D. lapponica*, frequently exist in harsh environments in alpine, subpolar, and polar regions globally (Körner, 1995) and have adapted to tolerate these conditions with densely packed vegetative growth (Cavieres et al., 2007). This structural adaptation appears to be beneficial not only to the survival of the individual plant, but to other species that establish themselves within and in proximity of the cushion. This is often

referred to as nurse plant theory (Niering et al., 1963; Cavieres et al., 2014), meaning that one plant species can facilitate or ameliorate conditions for another species (Callaway, 2007).

We incidentally observed *D. lapponica* individuals on the Avalon Peninsula appear to exhibit nurse plant characteristics observed in more northerly, arctic populations, suggested by the establishment of species within cushions. This type of facilitation often exists when the level of stress in an ecosystem is high (Navarro-Cano et al., 2015; Zvereva & Kozlov, 2007). Harsh environments pose limitations to growth due to extreme temperatures, high wind speeds, freezethaw cycle, or restricted growing seasons and create a high stress growing environment that requires adaptations for survival (Körner & Larcher, 1988). The barren Avalon Peninsula ecosystem where *D. lapponica* is present is such a harsh environment.

We observed that several different species had established and were growing interspersed in the dead and living tissue of *D. lapponica* (Figure 2. 15). Many woody evergreen and herbaceous species (Table A. 1) such as *V. uliginosum, E. nigrum, C. canadensis, S. tridentata* and *B. abies* were found here, suggesting that *D. lapponica* cushions do not create habitat restricted (selective) to particular species. A next research step would be to quantitatively assess the plant communities within cushions and examine their life history traits to determine whether they would be likely to colonize the barrens in the future under less harsh climate conditions.



**Figure 2. 15.** Example of incidentally observed species within the dead and living tissue of *D*. *lapponica*. Species include *K. angustifolia*, *S. tridentata*, *V. vitis-idaea*, fruticose lichen, and grasses.

All species observed in proximity (within each site) to *D. lapponica* were native species. However, it is possible non-native or even invasive species could take advantage of *D. lapponica*'s self-produced hospitable microclimate. Elsewhere, nurse plants have been documented to assist in non-native species colonization. For example, Cavieres et al. (2007) found that in the high alpine of the Chilean Andes mountains, the native nurse plant species *Azorella monantha*, could facilitate the colonization of non-native species. This establishment could potentially be detrimental to the local plant communities in that many native high alpine species are very specialized for their environment and therefore, do not have other areas in the region where they could persist if outcompeted. The morphological or physiological traits that make these species specialized to survive the harsh elements of their habitat also come with a biological trade-off in the form of lower competitive ability elsewhere (Day & Scott, 1981). In combination with their lower competitive abilities, the capacity of nurse plants to facilitate establishment of highly competitive, commonly generalist, non-native species such as *Trifolium* spp. and *Pilosella* spp. on the Avalon Peninsula (Sullivan, 2020) may compound their demise.

Although facilitation of non-native species establishment can have negative implications for native cushion plants, cushion plants can have a positive impact on local arthropods and pollinators, reducing the effects of environmental stress (Reid & Lortie, 2012). This impact could have important implications on both upper and lower trophic levels, as arthropods are able to provide nutrients through decomposition to cushions that they use as refuge. These additional nutrients would be beneficial in increasing plant health by potentially providing a great flower set for pollinators. Increasing pollination of cushion plants may also promote greater pollination of fruit-bearing species growing within the cushion such as V. uliginosum or V. vitis-idaea, both observed within D. lapponica cushions on the Avalon Peninsula. These species are essential food for a number of vertebrate species, including humans (Reid & Lortie, 2012). Newfoundlanders have a long history of foraging for a wide selection of berries including blueberry (V. angustifolium; V. uliginosum), partridgeberry (V. vitis-idaea), cranberry (V. oxycoccus), and bakeapple (R. chamaemorus), all of which would likely benefit from healthy pollinators and in return foster successful pollinator populations. The bee population on the island of Newfoundland is currently disease-free (Newfoundland and Labrador Beekeeping Association, 2020), while many bee colonies across the globe are in decline (Nowierski, 2021). This suggests a great need for protection of both these populations and the habitats that foster healthy pollinators in a variety of ecosystem types across the island.

# 2.4.2 Community-scale characteristics

Plant community assemblages can vary for many different reasons. Environmental stress can create physiological challenges that result in the selection of species that make up a community (Michalet et al., 2006). As well, topography of a landscape limits the types of species that can persist, depending on their moisture and nutrient requirements (Mata-Gonzalez et al., 2021). These abiotic factors, which often restrict the success of species' persistence, is called environmental filtering (Kraft et al., 2015).

Variation in rock cover and species richness influences the occurrence of *D. lapponica*, but not its abundance. Our observations of *D. lapponica* lead us to characterize it as a 'goldilocks' species, in that it needs a very specific set of requirements, which are not too far in one extreme of conditions or the other, in order to survive. We found *D. lapponica* more frequently in areas where the ratio between vascular plant richness and amount of rock cover is relatively equivalent, i.e., not too rocky and not too many additional species to compete with (Figure 2. 10). However, *D. lapponica* was found less frequently in the areas where rock cover or vascular species richness significantly dominate ground cover. We also found that where *D. lapponica* has established, there is no interactive effect of vascular species richness and rock cover and the cover, i.e., abundance of *D. lapponica* (

### Table 2. 2.)

Across the gradient of microhabitat characteristics examined, *D. lapponica* was not found at either extreme. At one extreme, areas of high rock cover are inhospitable to plants, and supported only crustose lichens. At the other, areas of high vascular plant richness suggest higher productivity, hence higher levels of competition. The areas of relatively high species richness suggest there is a greater availability of nutrients, soil for rooting, and moisture and, in turn, that

these microsites are more hospitable to less resilient plant species. Although not always the case, these species have relinquished less of their productivity in a physiological sense, meaning they are more vigorous and competitive (Woodward & Pigott, 1975).

Because D. lapponica is adapted to harsh arctic-alpine environments, physiological tradeoffs for this adaptation have resulted in a slow-growth tendency, which in turn limits its ability to compete with more vigorous species (Day & Scott, 1984; Molau, 1997). Our study barrens on the Avalon Peninsula are composed of highly resistant granitic parent material (Catto, 2020) and are characteristic of harsh environments that are heavily windswept, have regular frost disturbance, limited soil, and are commonly dominated by exposed rock. These are challenging environmental conditions for most plants, but we have identified microsites that are ideal habitat for *D. lapponica* (Day & Scott, 1981). Considering the ratio between vascular richness and rock cover that is associated with the occurrence of D. lapponica, the mid to low species richness and mid rock cover microsites found in the Avalon barrens are habitable for *D. lapponica* but are not hospitable for a number of competitive species (Figure 2. 10). D. lapponica did not occur in the same plant communities as C. calyculata, R. groenlandicum, and K. polifolia, which have higher moisture requirements and are generally found in the lower lying areas of our sites (Figure 2.9). Thus, we expect that the persistence and future establishment of *D. lapponica* will require the maintenance of low-competition microsites with moderate rock cover.

On the Avalon Peninsula, varying environmental gradients have the specific climate requirements for ideal *D. lapponica* habitat, but the geology/glacial history of the geographical features present differ somewhat. For example, the Hawke Hills sites have more extensive barrens that resemble a plateau with regular frost disturbance (Sutton et al., 2006). The edges of this environmental gradient are farther from the "summit", meaning the effects of encroachment

by less resilient species are not observed as frequently (Figure 2. 16). However, in the Avalon Wilderness Reserve, the presence of *D. lapponica* was limited to protruding higher elevation outcrops (Figure 2. 17). This topography means that the edge of the environmental gradient is closer to the "summit" of the barrens, and we more frequently observe encroachment by less resilient species. When setting up our plant community composition transects, we laid them out to capture as much site variation which generally followed the gradients described above. Although *D. lapponica* persists in both locations through environmental filtering, this same environmental filtering creates slightly different dynamics when it comes to competition and facilitation between species.



Figure 2. 16. Typical Hawke Hills site.



**Figure 2. 17.** Typical Avalon Wilderness Reserve site on top of an outcrop overlooking South West Pond often surrounded by lowlands of balsam fir and eastern larch forests, as well as wetland.

## 2.4.3 Regional-scale characteristics

Our analysis of *D. lapponica*-associated plant communities revealed associations with both latitude and elevation across its eastern North American range. At northern latitudes, in subarctic and arctic ecosystems, environmental conditions can limit the productivity of tundra ecosystems through cold temperatures with little precipitation and high winds, shorter growing seasons, frequently disturbed soil due to freeze-thaw cycles, shallow soils, and restricted soil moisture and nutrients. Combined, these factors create an extremely harsh environment where only select species have adapted to survive. In contrast to more southerly, temperate regions, often these abiotic stresses lead to interspecific facilitation as opposed to competition (Bertness & Callaway, 1994; Callaway & Walker, 1997). Since *D. lapponica* is a slow-growing species, adapted to these conditions, it makes sense that we would see it occur within a wide array of plant communities at higher latitudes, where it experiences far less competitive pressure. At lower latitudes, however, environmental conditions become more hospitable for plant species, creating more competitive pressure at similar elevations (Alexander et al., 2015). There, we observed an association between the types of plant communities *D. lapponica* is associated with and elevation. Slow-growing plants are often found predominantly at high elevations of alpine ecosystems where soil stability, moisture and nutrients are impacted by high winds (Urbanska & Chambers, 2002). These harsh environments are uninhabitable for more temperate, low-elevation species which are not adapted to these environmental conditions.

Plant communities that include D. lapponica on the Avalon and Northern Peninsulas of Newfoundland and Labrador have characteristics that fall between those of high and low latitudes with the species' eastern North American range. The clustering of Newfoundland sites in our NMDS analysis (Error! Reference source not found.) suggests that there is less variation in community composition within each of these sites than within sites across Nunavut or across the northeastern United States. Across the latitudinal gradient, the high latitude observations and lowest latitude (of its range) observations have greater variations in plant communities associated with *D. lapponica*, whereas the low to mid latitude observations have limited variation. The island of Newfoundland is close to the southern edge of D. lapponica's range, but it is not found in areas of high elevation, unlike the alpine habitats where it grows in the rest of the most southern part of its range. Although the area of Nunavut is quite large and the different regions noted were dispersed widely across the territory, we were still able to make comparisons of community composition. As well, even though the area in Newfoundland sampled was a smaller area, different parts of its whole range was captured, and it occurs in a much smaller area than Nunavut's populations. This suggests a combination of climate and other environmental factors such as substrate that make it suitable habitat.

We observed a wider variation in community composition at the northern sites (e.g., Nunavut, Northern Peninsula), likely because most of the habitat present is appropriate for D. *lapponica* to persist. At the southern edge of its range, the variation in plant communities is much smaller because the arctic-alpine species are limited to the "islands" of suitable habitat such as high elevation in mountain ranges as found in the Northeastern United States or significantly exposed regions such as the maritime barrens ecoregion in Newfoundland. Not only can the maritime barrens be considered terrestrial habitat islands within an expanse of boreal forest, but Newfoundland also itself is a true island, with an even more reduced species pool from the main regions of *D. lapponica* dispersion. There may also be more homogenous communities associated with *D. lapponica* on the island of Newfoundland because of its isolation from the mainland, which in turn creates a barrier to dispersal of many other species that may be well adapted to occur in concert with *D. lapponica*. We speculate that this isolation and in turn smaller species pools may mean lower resilience in the face of anticipated climate change in eastern Newfoundland (Finnis, 2013; Finnis & Daraio, 2018). Due to land use changes such as the more extensive development of power lines and the associated road near the Hawke Hills through to the Soldiers Pond Converter Station by 2017 (Nalcor Energy, 2014; Gorelick et al., 2017), and climate changes, as well as the pre-existing severe and isolated environment of the barrens, this Avalon Peninsula population is vulnerable.

# 2.4.4 The future of D. lapponica on the Avalon Peninsula

We have shown that the ideal habitat for *D. lapponica* is restricted to patches of microhabitat on parts of the barrens on the island of Newfoundland. These are areas experiencing ongoing climate change and human activities. While some are provincially and legally protected, including Hawke Hills Ecological Reserve and the Avalon Wilderness Reserve, there are still a

variety of human activities including ATVing, hiking, hunting, and research that occur, legally and illegally, in these areas. For *D. lapponica* to continue to persist on the Avalon Peninsula, these microhabitats need to be maintained, and left undisturbed to allow for natural disturbances to dominate.

By comparing the Newfoundland populations to those across *D. lapponica*'s northeastern North American range, we have put the Newfoundland populations into the broader context of its entire distribution. Climate change is projected to increase growing degree days and daily mean temperature, particularly in the winter, on the Avalon Peninsula (Finnis & Daraio, 2018). This would make it similar to more southerly locations with less harsh environments, which would increase competition. As a result, these populations may be placed at further risk. As well, because Newfoundland is an island with potentially limited or no source population, and unlike in alpine areas of the southern range edge where the species may be able to shift upwards, *D. lapponica* already persists at the highest elevations here and in turn, have nowhere else to go. However, it is possible the severe winds experienced on the barrens will continue to limit the ability of more competitive species to thrive.

#### 2.4.5 Conclusions

*D. lapponica* on the Avalon Peninsula exhibits attributes typical to arctic-alpine adapted species, creating its own microhabitat and facilitating the establishment of other species. The microhabitat it creates may mean that it could act as facilitator to species encroachment of more traditionally "boreal" species as well as non-native species, and we expect this to be more likely in Avalon Wilderness Reserve, where *D. lapponica*'s ideal habitat is restricted to small patches, than the in the more extensive barrens of the Hawke Hills. We characterized the ideal microhabitats for *D. lapponica* to be those that have some bare rock, and some additional

vascular species present, but not a high coverage of either. This ideal habitat is present in isolated patches on the Avalon Peninsula and should be protected to maintain the occurrence of this unique species to the island.

# 2.5 References

- Alexander, J. M., Diez, J. M., & Levine, J. M. (2015). Novel competitors shape species' responses to climate change. *Nature*, *525*(7570), 515-518.
- Arroyo, M. T. K., Cavieres, L. A., Peñaloza, A., & Arroyo-Kalin, M. A. (2003). Positive associations between the cushion plant *Azorella monantha* (Apiaceae) and alpine plant species in the Chilean Patagonian Andes. *Plant Ecology*, 169(1), 121-129.
- Badano, E.we., Jones, C.G., Cavieres, L.A., & Wright, J.P. (2006). Assessing impacts of ecosystem engineers on community organization: a general approach illustrated by effects of a high-Andean cushion plant. *Oikos*, *115*(2), 369-385.
- Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology* & *Evolution*, 9(5), 191-193.
- Bliss, L. C. (1963). Alpine plant communities of the presidential range, New Hampshire. *Ecology*, 44(4), 678-697.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling.*The R Journal*, 9(2), 378–400. <u>https://journal.r-project.org/archive/2017/RJ-2017-066/index.html</u>
- Callaway, R. M. (2007). *Positive interactions and interdependence in plant communities*. Springer Science & Business Media.
- Callaway, R. M., & Walker, L. R. (1997). Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, 78(7), 1958-1965.
- Catto, N. R. (2020). The Avalon of Newfoundland: geomorphology, people and landscape. In *World Geomorphological Landscapes* (pp. 333–367).
- Cavieres, L. A., Peñaloza, A., Papic, C., & Tambutti, M. (1998). Efecto nodriza del cojín Laretia acaulis (Umbelliferae) en la zona altoandina de Chile central. *Revista Chilena de Historia Natural*, *71*, 337-347.

- Cavieres, L. A., Badano, E. I., Sierra-Almeida, A., & Molina-Montenegro, M. A. (2007). Microclimatic modifications of cushion plants and their consequences for seedling survival of native and non-native herbaceous species in the high Andes of central Chile. Arctic, Antarctic, and Alpine Research, 39(2), 229-236.
- Cavieres, L. A., & Badano, E. I. (2009). Do facilitative interactions increase species richness at the entire community level? *Journal of Ecology*, 97(6), 1181–1191.
- Cavieres, L. A., Brooker, R. W., Butterfield, B. J., Cook, B. J., Kikvidze, Z., Lortie, C. J., ... & Callaway, R. M. (2014). Facilitative plant interactions and climate simultaneously drive alpine plant diversity. *Ecology Letters*, *17*(2), 193-202.
- Chen, J., Li, Y., Yang, Y., & Sun, H. (2017). How cushion communities are maintained in alpine ecosystems: A review and case study on alpine cushion plant reproduction. *Plant Diversity*, 39(4), 221-228.
- Damman, A. W. H. (1976). Plant distribution in Newfoundland especially in relation to summer temperatures measured with the sucrose inversion method. *Canadian Journal of Botany*, 54(13), 1561-1585.
- Day, R. T., & Scott, P. J. (1981). Autecological aspects of *Diapensia lapponica* L. in Newfoundland. *Rhodora*, 83(833), 101-109
- Day, R. T. & Scott, P.J. (1984). The biology of *Diapensia lapponica* in Newfoundland. *Canadian Field-Naturalist*, 98, 425-439.
- Driscoll, J. (2006). *Ex situ conservation protocols for the rare plants Braya longii (endangered), Braya fernaldii (threatened)(Brassicaceae) and Salix jejuna (endangered)(Salicaceae) endemic to the limestone barrens of Newfoundland* (unpublished MSc thesis, Department of Biology, Memorial University of Newfoundland, 126 pp).
- Finnis, J. (2013) Projected impacts of climate change for the province of Newfoundland and Labrador. Technical report submitted to: The Office of Climate Change, Energy Efficiency & Emissions Trading. St. John's: Provincial Govt. of Newfoundland and Labrador.
- Finnis, J., Daraio, J. (2018) Projected impacts of climate change for the province of Newfoundland and Labrador: 2018 update. Technical report submitted to: The Office of Climate Change, Energy Efficiency & Emissions Trading. St. John's: Provincial Govt. of Newfoundland and Labrador.
- Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., & Moore, R. (2017). Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*.

- Graae, B. J., Vandvik, V., Armbruster, W. S., Eiserhardt, W. L., Svenning, J. C., Hylander, K., ... & Lenoir, J. (2018). Stay or go-how topographic complexity influences alpine plant population and community responses to climate change. *Perspectives in Plant Ecology*, *Evolution and Systematics*, 30, 41-50.
- Guo, F., Lenoir, J., & Bonebrake, T. C. (2018). Land-use change interacts with climate to determine elevational species redistribution. *Nature Communications*, 9(1), 1-7.
- Hobbs, R. J., Higgs, E. S., & Hall, C. (2013). Novel ecosystems: intervening in the new ecological world order. John Wiley & Sons.
- Kevan, P. G., Forbes, B. C., Kevan, S. M., & Behan-Pelletier, V. (1995). Vehicle tracks on high Arctic tundra: their effects on the soil, vegetation, and soil arthropods. *Journal of Applied Ecology*, 655-667.
- Körner, C. H. (1995). Alpine plant diversity: a global survey and functional interpretations. In Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences (pp. 45-62). Springer, Berlin, Heidelberg.
- Körner, C., & Larcher, W. (1988, January). Plant life in cold climates. In *Symposia of the Society for Experimental Biology* (Vol. 42, pp. 25-57).
- Kraft, N. J., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, 29(5), 592-599.
- Larcher, W., Kainmüller, C., & Wagner, J. (2010). Survival types of high mountain plants under extreme temperatures. *Flora-Morphology*, *Distribution*, *Functional Ecology of Plants*, 205(1), 3-18.
- Mata-González, R., Averett, J. P., Abdallah, M. A., & Martin, D. W. (2021). Variations in Groundwater Level and Microtopography Influence Desert Plant Communities in Shallow Aquifer Areas. *Environmental Management*, 1-16.
- Michalet, R., Brooker, R. W., Cavieres, L. A., Kikvidze, Z., Lortie, C. J., Pugnaire, F. we., ... & Callaway, R. M. (2006). Do biotic interactions shape both sides of the humped-back model of species richness in plant communities?. *Ecology Letters*, 9(7), 767-773.
- Molau, U. (1996). Climatic impacts on flowering, growth, and vigour in an arctic-alpine cushion plant, *Diapensia lapponica*, under different snow cover regimes. *Ecological Bulletins*, 210-219.
- Molau, U. (1997). Age-related growth and reproduction in *Diapensia lapponica*, an arctic-alpine cushion plant. *Nordic Journal of Botany*, *17*(3), 225–234.

- Nalcor Energy (2014, May). *Muskrat Fall project: Soldiers Pond site*. Soldiers Pond info sheet. https://muskratfalls.nalcorenergy.com/wp-content/uploads/2013/03/Soldiers-Pond-Info-Sheet\_May2014.pdf
- Navarro-Cano, J. A., Verdú, M., García, C., & Goberna, M. (2015). What nurse shrubs can do for barren soils: rapid productivity shifts associated with a 40 years ontogenetic gradient. *Plant and Soil*, *388*(1), 197-209.
- Newfoundland and Labrador Beekeeping Association (2020, September 8). A Varroa action plan for Newfoundland and Labrador. Newfoundland and Labrador Beekeeping Association. https://www.nlbeekeeping.com/varroa-action-plan
- Niering, W. A., Whittaker, R. H., & Lowe, C. H. (1963). The saguaro: a population in relation to environment. *Science*, *142*(3588), 15-23.
- Niskanen, A. K. J., Niittynen, P., Aalto, J., Väre, H., & Luoto, M. (2019). Lost at high latitudes: Arctic and endemic plants under threat as climate warms. *Diversity and Distributions*, 25(5), 809-821.
- Nowierski, R.M.(2021). *Pollinators at a crossroads*. U.S. Department of Agriculture. https://www.usda.gov/media/blog/2020/06/24/pollinators-crossroads
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., and Wagner, H. (2020). vegan: Community Ecology Package. R package version 2.5-7. <u>https://CRAN.R-project.org/package=vegan</u>
- Protected Areas Association of Newfoundland and Labrador (PAANL). (2008). Maritime barrens: Southeastern barrens subregion. *Newfoundland and Labrador Ecoregion Brochures*, (36), 4.
- Reid, A. M., & Lortie, C. J. (2012). Cushion plants are foundation species with positive effects extending to higher trophic levels. *Ecosphere*, *3*(11), 1-18.
- Robinson, J., & Hermanutz, L. (2015). Evaluating human-disturbed habitats for recovery planning of endangered plants. *Journal of Environmental Management*, *150*, 157-163.
- R Core Team (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Scott, P. J., & Day, R. T. (1983). Diapensiaceae: a review of the taxonomy. Taxon, 417-423.

South, R. (1983). *Biogeography and Ecology of the Island of Newfoundland* (Vol. 48). Springer Science & Business Media.

- Sutton, J. T., Hermanutz, L., & Jacobs, J. D. (2006). Are frost boils important for the recruitment of arctic-alpine plants?. *Arctic, Antarctic, and Alpine Research, 38*(2), 273-275.
- Urbanska, K. M., & Chambers, J. C. (2002). 16. High-elevation ecosystems. In *Handbook of ecological restoration* (Vol. 2, pp. 376-400). Cambridge University Press Cambridge.
- Woodward, F.we. & Pigott, C.D. (1975). The climatic control of the altitudinal distribution of Sedum rose a (L.) scop. and S. telephium L. *New phytologist*, *74*(2), 323-334.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R* (Vol. 574). New York: Springer.
- Zvereva, E. L., & Kozlov, M. V. (2007). Facilitation of bilberry by mountain birch in habitat severely disturbed by pollution: Importance of sheltering. *Environmental and experimental botany*, *60*(2), 170-176.

#### **Chapter 3: Summary and conclusions**

## **3.1** Summary of findings

Arctic-alpine ecosystems are increasingly vulnerable due to global climate and potentially exacerbating land use changes. These plant communities are known for their resilience to the selective pressures relating to their climate, geology, and glacial history. While some arctic and alpine community characteristics are universal, there are variations in many regional characteristics, providing an opportunity to compare arctic-alpine flora. On the Avalon Peninsula of Newfoundland, the Maritime Barrens ecoregion is unique in that it is home to several arctic-alpine species, including the cushion plant, *Diapensia lapponica*, occurring at relatively low elevation (maximum 350 m) within a mid-boreal climate. While aspects of *D. lapponica* have been studied on the Avalon Peninsula and the island of Newfoundland, we recognized the opportunity to contribute empirical knowledge with respect to how *D. lapponica* plays a role within a hierarchy of habitats that *D. lapponica* is a part of, on a local (Avalon Peninsula) or regional (eastern North America) scale, and the microhabitat which it creates.

This thesis examined two abiotic factors that are associated with the persistence of *D*. *lapponica* on the Avalon Peninsula, microclimate and microtopographical features. We assessed the ability of *D. lapponica* to create a microhabitat through the measurement of ground temperature. The temperature under the base of *D. lapponica*'s cushion was marked by fewer extremes compared with the temperatures measured under other ground cover types. This suggests that *D. lapponica* can ameliorate temperature as a nurse plant, providing a microhabitat to more herbaceous flora. After observing that *D. lapponica* seemed to be associated with locally higher microtopography early in our field research, we qualitatively observed the

microtopographical features (crevice, flat, mat, mound) and general type of ground cover (rock, covered rock, vegetation) found frequently associated with *D. lapponica*. Our findings show that *D. lapponica* is most frequently found on mounds, although we did not detect a particular association with rock, covered rock, or vegetation.

Our further investigations examined the community composition associated with *D. lapponica*. We first assessed the percent cover of vascular plant species, bryophytes, and other ground cover (i.e., rock) to define plant communities associated with *D. lapponica* in a multivariate analysis. Most species frequently found in communities where *D. lapponica* was present are woody plant species, or those that require limited water and soil, including *Sibbaldiopsis tridentata* and *Kalmia procumbens*, as well as fruticose and crustose lichens, and rock. It is possible that some lichens categorized as crustose may actually be small stature foliose, but does not affect our findings. Species found in communities most dissimilar to those that had *D. lapponica* present included species such as bog rosemary, leatherleaf, and several other hydrophilic vascular plant species, as well as pleurocarpous mosses. In relation to the overall ground cover preferences, we also determined that *D. lapponica* prefers habitats where there is not too much rock coverage or limited vascular plant richness, likely due to its lesser ability to compete because of its slow growth.

Although the focus of this thesis was to understand the biotic and abiotic factors associated with the persistence of *D. lapponica* on the Avalon Peninsula, we wanted to compare this plant community to other locations regionally across eastern North America. The plant communities associated with the presence of *D. lapponica* follow latitudinal and elevational gradients, where more southerly sites such as New York, New Hampshire, Maine, and Vermont, are associated with higher elevations and hardier herbaceous and ericaceous alpine species

including *S. tridentata, Rhododendron* spp. and *Vaccinium* spp., while more northerly populations such as those in Nunavut are associated with higher latitudes and low-stature ericaceous and woody species including sedges, *Arctous* spp., *Cassiope tetragona.*, and *Oxytropis* spp.. The Avalon and Northern Peninsulas of Newfoundland populations are associated with plant communities including a mix of the different species for both regions including *Arctous* spp., *Alnus alnobetula, K. procumbens*, and *S. tridentata*, and is relatively centrally located in terms of latitude.

Examining the plant communities and abiotic factors that offer suitable habitat for *D*. lapponica on the Avalon Peninsula and across eastern North America provides insight into how this cushion plant species plays an important role as a nurse plant for less hardy species in a number of ways. Cushion plants like D. lapponica may provide protection from environmental stresses, facilitating biodiversity by providing refuge for other plants to establish. On the Avalon Peninsula, given the highly localized distribution of barrens habitat, appropriate habitat for D. *lapponica* may become limited, especially if it is further affected by climate and land use changes. Upslope range shifts are common among high alpine species under ongoing climate change, as their competitors overtake their lower-elevation range edges (Alexander et al., 2015). Given the proximity to the coast, it is likely that predicted increases in temperatures, for example, on the Avalon Peninsula, will be somewhat ameliorated (Finnis & Daraio, 2018) suggesting that potential changes may not be as severely detrimental to these populations as in other areas of its range. In areas in the southern edge of *D. lapponica*'s range, such as the Avalon Peninsula, populations already occur at high, and often the highest, elevations. We infer that the lack of upslope habitat will put these populations under further pressure as competitors squeeze their distributions as they move upslope under ongoing climate change. In sum, D. lapponica

populations in the southern end of its range may have nowhere to go as they are outcompeted in their current distributions.

Throughout this thesis, we built upon the fundamental observational field work of Day and Scott (1981; 1984), as well as Damman (1976) who described where *D. lapponica* persists on the island of Newfoundland and the general life history of the species. Here, our research provides important empirical findings on the association of ground cover, microtopography, and microclimate with the way that *D. lapponica* persists on the Avalon Peninsula.

## **3.2 Implication of findings**

Given their slow-growing tendencies and ability to persist in harsh environments, it is important to consider cushion plants such as D. lapponica for long term monitoring projects as bioindicators of climate change. Large parts of these species' ranges occur in regions of the planet that are predicted to see the greatest changes due to climate change (e.g., subarctic, high alpine, etc.) and therefore, it is important to monitor species that are highly specialized and adapted to the historic conditions in these environments. This monitoring is especially important considering the suitability of cushion plants to perform as nurse plants for less well-adapted species, and as bioengineers by way of physical protection and retention of necessary resources in ecosystems where resources are limited. Not only do we expect immediate protection for newly established herbaceous species within *D. lapponica* and other cushion species, but cushion plants may be suitable as refugia for seed source populations of other species. These small refugia supporting parent populations of other species, may eventually facilitate the colonization of landscapes with little to no vegetation once the environmental and seed bed conditions surrounding the cushions have more amenable growing conditions. If we consider cushions as refugia in this way, it becomes apparent that the landscape is primed for the dispersal and
establishment of less hardy species into unoccupied patches once environmental conditions become favourable. The facilitation of colonization by *D. lapponica* will continue to maintain and potentially increase biodiversity, albeit potentially to their own detriment, as described below.

*D. lapponica* is found most frequently in areas on the Avalon Peninsula where some other plant species and some rock cover occur, but not a substantial amount of either. Slowgrowing species such as *D. lapponica* have a hard time competing, and therefore thrive in areas that are not highly biologically diverse. With climate change, there is the potential for encroachment of more competitive species, including non-native and invasive species, moving upslope as conditions become more conducive to higher primary productivity. By creating nurse habitat for encroaching species, *D. lapponica* may in fact facilitate their own out-competition. Land use for development of energy transmission and recreation may play a role in the long-term persistence of *D. lapponica* on the Avalon Peninsula. Disruption or segmentation due to ATV use and development of roads for powerline infrastructure may cause the loss of appropriate barrens habitat or changing of abiotic factors (e.g., substrate size) for *D. lapponica* and several specialized plant species (e.g., *K. procumbens, Arctous alpina, Racomitrium* spp.). We have shown in this thesis that *D. lapponica* cannot occur where diversity and competition are high, so maintaining and protecting the barrens habitat is critical for their conservation.

This is not only of importance from a global perspective but in considering the protection of *D. lapponica* habitat regionally and even globally. We found that the populations of *D. lapponica* and their associated plant communities in our study followed a latitudinal gradient with the majority of community variation in the arctic (regions of Nunavut) and alpine (northeastern United States) regions. The Intergovernmental Panel on Climate Change (IPCC)

suggests that arctic-alpine environments are at risk for the most changes due to climate change which includes the majority of *D. lapponica* habitat worldwide. Although there is not a concise answer as to how climate change will impact these areas, there are observed changes such as novel competitors, invasive species, and alterations to primary productivity of certain species. This implies that the *D. lapponica* could see an increasingly limited suitable habitat or challenges in its persistence over the coming decades.

### 3.3 Study considerations and limitations

One major limitation was logistical constraints due to COVID-19 travel restrictions. Ideally, we would have visited every population of *D. lapponica* on the island of Newfoundland over the course of one full field season, which would have provided a gradient of different abiotic variables (e.g.,, climatic, elevation, latitude) to compare each of our microclimate measurements and observations of percent cover. However, because of travel restrictions resulting from the COVID-19 pandemic, we switched approaches when it came to comparing different sites and asked researchers who had previously studied *D. lapponica* for data. Therefore, instead of personally going to the Long Range Mountains, we used data previously collected by other researchers including: Paul Sokoloff (Canadian Museum of Nature); Zoe Panchen (University of British Columbia); Sergei Ponomarenko (Canadian Museum of Nature); Anna Crofts (Université de Sherbrooke and formerly Memorial University); and Georgia Murray (Appalachian Mountain Club), or within citizen science applications upon suggestion of the above researchers. This approach limited the ability to obtain full percent cover assessments in sites with and without *D. lapponica*, in turn limiting the statistical scope of this analysis. Ideally, future studies would collect *D. lapponica* occurrence data with the variables we studied at our Avalon Peninsula sites. As well, given the slow-growth of many arctic-alpine communities, it

would be preferred to complete a longer-term version of this study to incorporate revisitation, for example, every five years, for population assessment and to assess encroachment of other species, which is outside the scope of a Master's project.

#### **3.4** Future study suggestions

We approached the study and assessment of *D. lapponica* on the Avalon Peninsula from a hierarchical perspective. We viewed the cushion of *D. lapponica* itself as a habitat for other plant species, which was within a subset of habitat and associated plant communities across the landscape that is generally known as the Maritime Barrens Ecoregion of the Avalon Peninsula, and these pockets of suitable *D. lapponica* habitat on the Avalon Peninsula are part of a range of other suitable but not identical habitat across Eastern North America. Future research on *D. lapponica* and associated communities should consider this hierarchical framework, as we have demonstrated key characteristics of individuals, populations, and communities that may inform our understanding of community assembly dynamics in the future.

A potential future study could examine age-growth relationships for Newfoundland *D. lapponica* populations for comparison to populations in northern Sweden aged by Molau (1997). Although we did measure the diameter of *D. lapponica* cushions at our Avalon Peninsula sites, we found that the fitted growth curve produced by Molau (1997) did not fit well with the data that we collected. This could potentially have to do with the different climates and growing degree days influencing primary productivity. Therefore, we would suggest doing a more thorough examination of the age of *D. lapponica* in populations across eastern North America involving both diameter measurements of cushions, as well as attempting to determine plant age using dendrology, given its woody stem. Examining a number of sites along a latitudinal gradient would be important for statistical analysis, particularly for development of an alternative fitted

growth equation. Aging and comparing ages between different areas of a species range are important for constructing current distribution, but may contribute to assessing how populations, especially those that are highly adapted to certain ecosystems, will respond to climatic variations.

Another possible study would look explicitly at cushions as seed sources for other flora, as suggested by the observed fostering of other species. It would be interesting to research the diversity gradient of other species away from the centre of cushions, as well as observing the abundance of each species, to better understand whether the establishment of other species also radiates from cushions. The diversity and abundance of other species in and around the cushion could help inform inferences made when modelling these alongside observations of cushion die-off. It may provide an idea of both the positive and negative effects associated with nurse plant activity. Both these studies would require long-term monitoring, e.g., assessments every five years as long as feasible, given the slow-growth habits of cushion plants as well as other species frequently found growing under severe environmental conditions.

An interesting study on the barrens of the Avalon Peninsula would be to better understand how linear disturbances including roads, ATV trails, hiking trails, and other anthropogenic development affect the substrate and the plant communities present. Sullivan (2020) investigated how natural and non-natural linear disturbances influenced the presence of non-native species in the boreal forest of Newfoundland. This type of study could be applied to a different type of ecosystem well. Other studies (Driscoll, 2006; Robinson & Hermanutz, 2015; Sutton et al., 2006) found that specialized and highly adapted barrens species could be affected by alterations to substrate size, causing a hindrance to establishment. Investigating how anthropogenic linear disturbances potentially alter the plant communities on the barrens will help inform further management recommendations and conservation efforts. Another interesting study

to consider at our populations of *D. lapponica* on the Avalon Peninsula would be to continue to complete long-term monitoring (e.g., every five years for as long as feasible) to include plant community composition assessment along with the collection of portable weather station data. This might provide a more realistic prediction for the fate of arctic-alpine species on the Avalon Peninsula.

In terms of future study suggestions for *D. lapponica* in Eastern North America, it would be beneficial to conduct field observations where *D. lapponica* persists in arctic-alpine and barren regions over a longer period of time. These communities could then be compared, allowing deeper investigation into different functional traits and roles of the different species in the community. In regions where the diversity is low and primary productivity is reduced due to environmental constraints, it would be interesting to determine whether each species has a role and how or if that influences community composition. Long-term monitoring of these different communities could be a vital case study of how *D. lapponica*, as a cushion plant, in different plant communities across its range over time, plays a role in its local ecosystem as it responds to climate change.

#### **3.5** Recommendations for management

Sixty percent of our study sites where *D. lapponica* is found on the Avalon Peninsula are within provincially protected areas (Hawke Hills Ecological Reserve and Avalon Wilderness Reserve), which means that there are already protective measures put into place in terms of management practices. According to s. 24 of the *Wilderness and Ecological Reserves Act* (1980) , there are several rules and regulations in place including the strict prohibition of: destruction or removal of plants, animals, and fossils; introduction of plants or animals; forestry and mining; powerline development; agriculture; new roads, tracks, or other construction; and driving any

type of vehicle. As well, hiking should be minimally destructive as possible. However, because of the expansive barrens landscape, regulation is difficult, and there is evidence of consistent recreational use which suggests that the importance of fostering positive local attitudes towards the landscape is vital. One management recommendation for these relatively isolated locations is to monitor the use of ATVs and foot along the trails through the reserves. As well, continuing to maintain and support provincially protected areas through educational activities, adaptive policy, and signage may aid in continued management practices and interest in protected areas across the Avalon Peninsula (Ward et al., 2018).

Long-term monitoring of plant communities associated with *D. lapponica* and climate variations on a regional scale is an important recommendation for management to provide an idea of how these plant communities are changing spatially and temporally in response to weather events and climate change. By having a consistent long-term monitoring study, practices within a management plan can be adjusted to best suit the conservation and protection needs of the species both now and in the future. Data can provide evidence to substantiate proposals for species at risk recovery planning.

Finally, one other management recommendation is the continuation of the collection of live *D. lapponica* samples globally for regional museums (e.g., The Rooms) or national museums (e.g., Canadian Museum of Nature) while ensuring as much information about associated plants, habitat description, and specific locations are recorded (Mann, 2001). As well, continuing to build on current online databases of collections (e.g., GBIF) is essential in a digital age for conservation and preservation. As well, the use of citizen science data from applications like iNaturalist could be very useful in helping to inform or add to management strategies based

on scientist-collected field data, aiding in monitoring and prioritizing sites for detailed investigation.

#### 3.6 Conclusion

D. lapponica is a distinctive arctic-alpine species that persists on the Avalon Peninsula of Newfoundland, and in suitable habitats across northeastern North America. Investigating its functioning within the local plant communities from a hierarchical perspective can help in interpretations of the species range on a regional scale. D. lapponica is capable of ameliorating extreme temperatures over the course of the warmest and coldest months on the Avalon Peninsula, which suggests it has an important role as a microhabitat provider for species less resilient to the environmental conditions. On a local scale, D. lapponica exists on isolated microtopography within the overall habitat, where there is an equivalent amount of species diversity and bare rock present which suggests a very specific set of requirements for persistence. Usually, these requirements include high ground, and relatively low to medium species diversity including those that are generally slow-growing species and are unlikely to be highly competitive. Given its slow-growth habit, D. lapponica is potentially more susceptible to encroachment by more competitive species with high primary productivity capabilities if environmental conditions become more suitable. It is possible that climate change and anthropogenic pressures may trigger movement of some previously lowland species moving upslope or environmental conditions no longer be suitable for D. lapponica. Current suitable habitats in other regions of its range are projected to be at the highest risk of impact due to climate change so current and future long-term monitoring is vital for conservation and preservation success. Personally, we hope its value as a unique arctic-alpine cushion plant leads

to its continued persistence and further protection on the island of Newfoundland, and its

enjoyment by hikers and botanists continues.

## 3.7 References

- Alexander, J. M., Diez, J. M., & Levine, J. M. (2015). Novel competitors shape species' responses to climate change. *Nature*, *525*(7570), 515-518.
- Damman, A. W. H. (1976). Plant distribution in Newfoundland especially in relation to summer temperatures measured with the sucrose inversion method. *Canadian Journal of Botany*, 54(13), 1561-1585.
- Day, R. T., & Scott, P. J. (1981). Autecological aspects of *Diapensia lapponica* L. in Newfoundland. *Rhodora*, 83(833), 101-109
- Day, R. T. & Scott, P.J. (1984). The biology of *Diapensia lapponica* in Newfoundland. *Canadian Field-Naturalist*, 98, 425-439.
- Driscoll, J. (2006). *Ex situ conservation protocols for the rare plants Braya longii (endangered), Braya fernaldii (threatened)(Brassicaceae) and Salix jejuna (endangered)(Salicaceae) endemic to the limestone barrens of Newfoundland* (unpublished MSc thesis, Department of Biology, Memorial University of Newfoundland, 126 pp).
- Mann, Henry. (2001). *Introductory Guide to the Collection and Preservation of Plant Specimens*. Sir Wilfred Grenfell College, Memorial University of Newfoundland, Corner Brook, NF.
- Molau, U. (1997). Age-related growth and reproduction in *Diapensia lapponica*, an arctic-alpine cushion plant. *Nordic Journal of Botany*, 17(3), 225–234.
- Robinson, J., & Hermanutz, L. (2015). Evaluating human-disturbed habitats for recovery planning of endangered plants. *Journal of Environmental Management*, 150, 157-163.
- Sullivan, J. (2020). *Come from away: non-native plant establishment within the boreal forest region of Newfoundland, Canada* (master's thesis, Memorial University of Newfoundland).
- Sutton, J. T., Hermanutz, L., & Jacobs, J. D. (2006). Are frost boils important for the recruitment of arctic-alpine plants?. *Arctic, Antarctic, and Alpine Research, 38*(2), 273-275.
- Ward, B. M., Doney, E. D., Vodden, K., & Bath, A. J. (2018). The importance of beliefs in predicting support for a South Coast National Marine Conservation Area in Newfoundland and Labrador, Canada. *Ocean & Coastal Management*, 162, 6-12.

Wilderness and Ecological Reserves Act, Royal Statutes of Newfoundland and Labrador (1980, c. W-9). Retrieved from the Office of the Legislative Counsel Newfoundland and Labrador website: https://www.assembly.nl.ca/legislation/sr/statutes/w09.htm

# Appendix

**Table A. 1.** List of dominant flora species/ground cover observed on barrens of the Avalon Peninsula, island of Newfoundland and additional species mentioned in the text.

Scientific Name	Common Name	Authority
Dominant species on the Avalor	Peninsula	Autority
Andromeda polifolia	hog rosemary	I
Aronia x prunifolia	chokeberry	(Marshall) Rehder
Chamaedanhne calvculata	leatherleaf	(I ) Moench
Cornus canadansis	bunchberry	I
	crustose lichen (ID unknown)	
Dianensia lannonica	L apland pincushion plant	I
Empersia imponica	black crowberry	L
-	fruticose lichen (ID unknown)	-
	induceose nenen (iD diikitowit)	
-	grasses (ID unknown)	-
Juniperus communis	common juniper	L.
Kalmia angustifolia	sheep laurel	L.
Kalmia polifolia	bog laurel	Wangenh.
Kalmia procumbens	alpine azalea	(L.) Gift & Kron & P.F.Stevens
1	1	ex Galasso, Banfi & F.Conti
Lycopodium spp.	clubmoss (genus level)	L.
Maianthemum canadense	Canada mayflower	Desf.
Myrica gale	sweet gale	L.
-	pleurocarpous moss (ID	-
	unknown)	
Polytrichum spp.	haircap mosses (genus level)	Hedw.
Rhododendron groenlandicum	Labrador tea	(Oeder) Kron & Judd
Sibbaldiopsis tridentata	three-toothed cinquefoil	(Aiton) Rydb.
Solidago uliginosa	bog goldenrod	Nutt.
Vaccinium angustifolium	lowbush blueberry	Aiton
Vaccinium uliginosum	northern bilberry, bog blueberry	L.
Vaccinium vitis-idaea	partridgeberry, lingonberry	L.
Other species mentioned		
Alnus alnobetula	green alder	(Ehrh.) K.Koch
Arctous alpina	alpine bearberry	(L.) Nied.
Berneuxia spp.	-	Decne.
<i>Betula</i> spp.	birch (genus level)	L.
Cassiope tetragona	Arctic white heather	(L.) D.Don
Draba nivalis	snow draba	Lilij.
Dryas spp.	mountain avens (genus level)	L.

Galax spp.	wandplant (genus level)	(Poir.) Brummit
Oxytropis spp.	locoweeds (genus level)	DC.
Pilosella spp.	hawkweed	Vaill.
<i>Pyxidanthera</i> spp.	-	Michx.
Racomitrium lanuginosum	hoary rock moss	(Hedw.) Brid.
Ranunculus glacialis	glacier buttercup	L.
Rhododendron tomentosum	northern Labrador tea	Harmaja
<i>Salix</i> spp.	willow (genus level)	L., nom. cons.
Shortia spp.	-	Torr. & A.Gray
Trifolium spp.	clover (genus level)	L.
Vaccinium oxycoccus	bog cranberry	L.