LIFE'S MORE THAN ONE NICHE: DEMOGRAPHIC CONSTRAINTS ON NORTHERN BLACK SPRUCE RANGE EXPANSION IN YUKON, CANADA

by © Katie Goodwin
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Abstract

Species' distributions are often characterized by the species' niche represented in geographic space. Species' niches can be divided demographically, resulting in multiple demographic niches with unique dimensions. This approach determines which life stages have either the narrowest niche breadth or the least available niche space at the range edge, and thus act as key demographic hurdles on range expansion. We quantified microsites inhabited by different life stages of black spruce (*Picea mariana*) at subarctic treeline in Yukon, Canada to characterize demographic niche breadth and assess how available niche space changed towards the range edge. We found that restricted suitable emergent niche space and viable seed availability towards the range limit were the overwhelmingly main limiting demographic bottlenecks on northern range expansion. Our findings suggest that demographic niches can identify life stage specific hurdles to range expansion, contributing to our understanding of how species' distributions will respond to climate change.

Keywords: species' distributions; treeline; demographic niches; ontogenetic niche shifts; seed production; seedling emergence; microsite suitability; subarctic; regeneration niche; *Picea mariana*

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I would like to dedicate my thesis to my nephew, Witt Goodwin, who inspires me to do my part in making the world a better place for future generations to enjoy.

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Co-Authorship Statement

Dr. Carissa Brown is a co-author on Chapters Two and Three. As principal author, I was the main contributor for 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 Dr. Brown who contributed to project design, data analysis, and manuscript preparation.

Chapter 1: Introduction and overview

1.1 Species' distributions in a warming world

What shapes a species' range? This seemingly simple question has long been asked by biogeographers and ecologists, unpacking a complex assemblage of factors that influence a species' ability to occur in a given location (e.g., Humboldt and Bonpland 1807; Connell 1961; McArthur 1972). Teasing through these factors to identify those that are most important for a particular population remains a fundamental research challenge, which will allow us to accurately predict where and when ranges may shift in the future.

Species' range limits have been found to correspond with their respective niche limits 46 - 77% of the time (Hargreaves et al. 2014; Lee-Yaw et al. 2016). A niche in this context refers to the range of ecological conditions a population requires to grow, survive, and reproduce within a given region (Grinnell 1917; Hutchinson 1957). This Hutchinson fundamental niche definition consists of a multidimensional hypervolume of environmental variables that species can maintain populations within (Hutchinson 1957). Discrepancies between fundamental niche limits and range limits are influenced by dispersal limitations and negative biotic interactions that prevent a species from occupying suitable niche space, and source-sink dynamics that maintain sink populations in unsuitable niche space (Pulliam 2000).

A subset of a species' niche, the climatic niche, is often considered the dominant driver in shaping species' distributions (Pearson and Dawson 2003). For example, the upper altitudinal or latitudinal limit where tree species can grow (henceforth treeline) is often described by a climatic boundary (Körner 2012). The treeline represents the ecotone from closed forest to treeless tundra, a transition that can span from a few metres to a few kilometres (Körner 2012). On a global scale, the treeline roughly correlates with the mean 10°C isotherm during the warmest month (Brockmann-Jerosch 1919 from Körner 2012). Although low temperature extremes are not a survival issue for treeline species, limited productivity due to frost damage, freeze-thaw related hydraulic failure, and mechanical damage have been proposed as explanations for temperature constraints on tree range expansion into tundra ecosystems (Körner 1998).

Given the importance of climate in shaping species' ranges, contemporary climate change is expected to cause range shifts as species follow their climatic niche (Chen et al. 2011). Although many species are spatially tracking their climatic niche in response to climate change (Chen et al. 2011), this is not a uniform trend (e.g., Harsch et al. 2009; Freeman et al. 2018). Subarctic and alpine regions, where treelines occur, are experiencing some of the most intense warming (Chapin et al. 2005; Pepin et al. 2015). Despite acute warming, only 52% of treelines are estimated to be tracking their climatic niche northward or to higher elevations (Harsch et al. 2009). Lack of range shifts may represent a lag effect where species have not yet had the time to establish in newly available niche space (Loarie et al. 2009; Rannow 2013), particularly relevant at treeline given the slow growth and long life span of treeline trees (Körner 2012). However, it is generally accepted that climate alone does not delineate species' ranges, particularly at local and regional scales (Holtmeier and Broll 2007). Several non-climatic abiotic and biotic variables have been found to impact tree distributions at treeline including nutrient availability (Sullivan and Sveinbjörnsson 2010), topography (Resler et al. 2005), seed predation (Jameson et al. 2015; Kambo and Danby 2017), competition (Wang et al. 2016), and facilitation (Germino et al. 2002; Renard et al. 2016). Many of these variables may also be indirectly influenced by climate (e.g., Hobbie et al. 2002; Alexander et al. 2016), further complicating species' responses to climate change.

At a landscape scale, these abiotic and biotic factors shape a species' distribution. However, the niche space an individual directly experiences happens at a much finer scale: its microsite. At this scale, substrates within a region are heterogeneous (Harper 1977), creating a wide variety of microsites in an area that may or may not provide suitable niche space for establishment. The abundance and ecological composition of suitable microsites at the treeline remain unclear (Brodersen et al. 2019); yet, for a range shift to occur, sufficient seed must disperse and reach suitable microsites for establishment. Additionally, mismatches can occur where a microsite that is suitable for one life stage may be unsuitable for a later life stage such as seed-seedling conflicts where higher seedling emergence occurs in areas of lower seedling survival (Schupp 1995; Cranston and Hermanutz 2013).

Mismatches in microsite suitability across an organism's life cycle show that abiotic and biotic factors can have different impacts on an individual throughout its life history, causing several demographic bottlenecks that can influence range shifts. The ability for sufficient trees to establish and reach reproductive maturity beyond the range depends on the relative intensities of these demographic bottlenecks. Limited seed availability can inhibit establishment (Sveinbjörnsson et al. 1996; Kroiss and HilleRisLambers 2015), and dispersed seed must land on a suitable substrate for germination (Dufour-Tremblay et al. 2012; Davis and Gedalof 2018). After germination, successful seedling establishment is also limited to specific microsites (Batllori et al. 2009; Renard et al. 2016). When seedlings mature to adulthood and emerge from the sheltered shrub layer, they are exposed to colder open air temperatures and higher winds, which can cause mortality (Wilson et al. 1987; Grace et al. 2002). Once adulthood is reached, existing populations may be maintained by vegetative reproduction, but sexual reproduction is required for range expansion (Malcolm et al. 2002) and is often limited at treeline (Krebs et al. 2012; Brown et al. 2019). Tree populations must surpass all of these demographic bottlenecks for range expansion to occur and the most limiting life stages will act as rate limiting steps for range expansion.

1.2 Demographic niches and range shifts

Identifying the rate limiting demographic bottlenecks on species' distributions can be achieved through the lens of demographic niches. Research on species' distributions usually estimate the niche at the species level (Smith et al. 2019; but see Bykova et al. 2012; Ghosh et al. 2016). Yet Grubb (1977) proposed that species have a regeneration niche; i.e., the range of environmental characteristics required for establishment. Indeed, a species' environmental requirements can change throughout its life cycle beyond establishment (Eriksson 2002; Quero et al. 2008); this is defined as an ontogenetic niche shift (Parrish and Bazzaz 1985). Although plants cannot move to more suitable habitat, they can respond in different ways to changes in environmental variables throughout their life cycle (Quero et al. 2008; Anderson et al. 2009). Therefore, the Hutchinson niche can be composed of unique hypervolumes representing a species' vital rates (e.g., fecundity, growth) or life stages (e.g., seedling, adult), creating multiple demographic niches (Maquire 1973; Pironon et al. 2018). Demographic niches further refine the relationship between a species' distribution and niche, where individuals can only exist within suitable niche space for their respective life stage.

Species can exhibit expanding, contracting, and directionally shifting niche breadths throughout their life cycle, and all three shift types can influence a species' distribution. An ontogenetic niche expansion occurs when earlier life stages have a narrower niche than later life stages. For example, juveniles can be more susceptible to stress or require greater resources than adult life stages (Anderson et al. 2009; Arieira et al. 2016). This restricts plant establishment to a subset of environmental conditions that later life stages could otherwise occupy. An ontogenetic niche contraction occurs when requirements are more strict at later life stages. In this instance, later life stages may require a narrower breadth of nutrient, water, or light availability (Quero et al. 2008; Bertrand et al. 2011). Niche contractions lead to widespread mortality of individuals as they pass to the narrowing life stage, potentially limiting range shifts. A directional ontogenetic niche shift involves partially non-overlapping requirements across life stages. For example, the presence of neighbouring plants may facilitate emergence, but as the individual establishes into a seedling, this relationship may switch to resource competition (Schupp

1995; Pérez-Ramos et al. 2012; Cranston and Hermanutz 2013). Directional niche shifts can lead to mal-adaptations and mortality as individuals pass to the later life stage. Characterizing a species' demographic niches can inform how that species' distribution may respond to climate change (Stohlgren et al. 1998; Donohue et al. 2010).

1.3 Thesis overview

Treelines species are not uniformly tracking their climatic niches northward and to higher elevations (Harsch et al. 2009). Understanding what influences the rate and direction of future range shifts is crucial to accurately predict where, and at what abundances, tree species will exist in the future. The relative availability of suitable microsites throughout a species' life cycle may create multiple demographic bottlenecks on establishment at the range limit. Using treeline black spruce (*Picea mariana* [Mill] BSP) populations in subarctic Yukon as a model system, here I show how demographic niches can aid in understanding the relative importance of demographic bottlenecks and microsite availability on species' distributions in a rapidly changing region. In Chapter Two, I characterized black spruce's demographic niches for four life stages (Box 1.1) to inform which life stage has the narrowest requirements, impeding range expansion. Chapter Three then presents how available niche space for each life stage changed across a gradient heading towards the range edge, highlighting key demographic constraints on range expansion.

Box 1.1 A description of the black spruce life stages assessed in this study.

Emergent: A recently germinated individual that is less than one year old.

Seedling: An individual ≤60cm tall.

Non-Reproductive Adult: An individual >60cm tall without reproductive structures (cones). Due to harsh conditions, range-edge populations of black spruce often exhibit stunted growth forms (krummholz) that can be reproductively mature despite their small stature (<2m); therefore, I considered any individual >60cm tall an adult.

Reproductive Adult: An individual >60cm tall with reproductive structures (cones)

Treeless Tundra: A 50 cm x 50 cm area of tundra in which no tree is present. This allows for comparison of the microsite each life stage is present in to the general tundra substrate.

In this thesis, the analytical approach used to construct demographic niches was ordination. Ordination provides views into high-dimensional space by reducing a large number of variables into fewer and easier to interpret reduced axes (McCune and Grace 2002; Zuur et al. 2007). Specifically, non-metric multidimensional scaling (NMDS), is a non-parametric ordination method that works well for ecological data that violate parametric ordination assumptions (McCune and Grace 2002). NMDS ordinates variables into reduced NMDS axes, where each individual is assigned a score along each NMDS axis to identify its location in ordination space (i.e., niche space in this context). Using NMDS, I quantified the microsites inhabited by individuals of different life stages along transects placed across the treeline ecotone heading towards the range edge. The cluster of scores each life stage occupied in niche space composed black spruce's demographic niches (Chapter Two; Fig. 1.1). For Chapter Three, individual's NMDS scores were plotted along this treeline gradient and compared to unoccupied microsites to identify changes in microsite availability towards the range edge (Fig. 1.1).

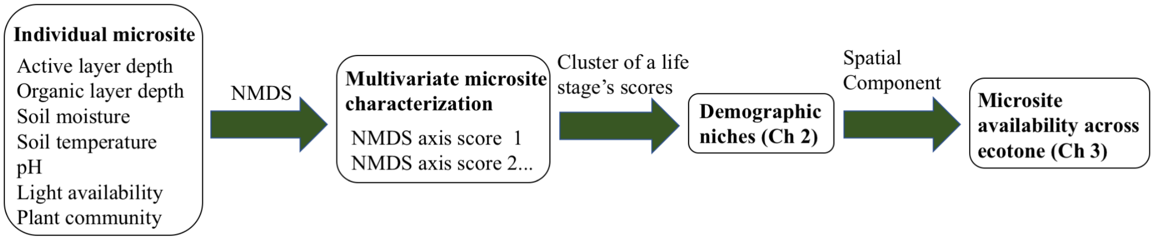


Figure 1.1 An overview of the methodological approach taken in this thesis. A series of microsite variables were captured at the base of individual trees of different life stages. NMDS ordinations formed a multivariate characterization of the microsite individuals occupy. The cluster of microsites occupied by individuals of a given life stage shaped black spruce's demographic niches. Then, NMDS scores of both occupied and unoccupied microsites were plotted along a spatial gradient to assess microsite availability across the treeline.

1.4 Model system

Annual average temperature in the Yukon has increased by 2°C in the past 50 years, twice the rate observed globally (Streicker 2016). This warming results in a rapidly changing region that is experiencing major landscape changes including increased forest fires, permafrost thaw, and species' range shifts (Streicker 2016). My thesis research was conducted at three study sites located along the Dempster Highway near Eagle Plains, Yukon (66° 22' 12" N, 136° 43' 48" W; Fig. 1.2). The region is characterized by rolling hills that dip above and below the treeline ecotone, thus creating a series of alpine treelines within the larger latitudinal treeline. Substrates are underlain with continuous permafrost with a seasonal thaw depth of less than 1 m (Tarnocai et al. 1993). This is a fire-prone landscape, with a fire return interval of ~80 - 150 years (Hu et al. 2006; Kasischke et al. 2010). Regular disturbances result in temporally changing available niche space, where fire periodically alters substrates by removing the plant community and organic layer, which then regenerate over time. Black spruce is the dominant tree species in the area and, as a fire-adapted species, will successively burn and regenerate during this cycle.

I considered a treeline site suitable for this study if it (1) was a black spruce-dominated stand; (2) contained all life stages included in this study; (3) exhibited gradually decreasing tree density heading upslope; and (4) was road accessible. Site One, located north of Eagle Plains is drier than the other sites with an understory shrub community primarily consisting of *Betula spp., Salix spp., Rhododendron spp., Vaccinium uliginosum, Empetrum nigrum, Vaccinium visis-idaea*, with a high lichen cover (primarily *Cladonia spp*.). Sites Two and Three, south of Eagle Plains, were wetter and moss dominated, primarily with *Sphagnum spp.* and feathermoss species (e.g., *Hylocomium* spp.), and interspersed with a similar shrub community to Site One. For a study map and detailed description of the three study sites, see Chapter Two.

Figure 1.2 Range map of black spruce (*Picea mariana*). Green region represents the range. Black circle represents my study region at the northern range limit in Yukon, Canada (modified from United States Geological Survey).

1.5 Model species

Black spruce is a coniferous species that is commonly found across North American boreal forests (Johnston and Smith 1985). Southern populations can reach up to 20 m in height, while northern populations often exhibited stunted growth forms (krummholz). Black spruce is a long-lived tree that can potentially persist up to 370 years (Trant et al. 2011). However, given the fire return interval of northern Yukon, trees likely never reach this age in our study area. Populations in the region begin producing cones when 25-30 years old, and reliably produce cones at 85 years (Black and Bliss 1980). Reproductive maturity can occur in krummholz individuals despite their small stature (<2 m). Black spruce is a semi-serotinous species and maintains an aerial seedbank containing several cone cohorts that will gradually release seed in the absence of fire and massively disperse after a fire (Zasada et al. 1992). Cones will experience at least one winter in the aerial seedbank before dispersal, thus, dispersed seeds have been cold stratified and are not dormant (Safford 1974; Black and Bliss 1980). Seeds are dispersed by wind and documented to travel up to 80 m from the windward edge of a mature stand (Johnston and Smith 1985). Once dispersed, black spruce seed loses its viability within 10 - 16 months (Fraser 1976). Black spruce can also reproduce asexually by forming adventitious roots on lateral branches to produce clonal stems (Holtmeier 2009).

1.6 Thesis objectives and significance

The goal of this thesis is to characterize black spruce’s demographic niches to inform microsite suitability and demographic constraints at treeline. In Chapter Two, I quantified the microsites that individuals of different demographic stages occupy to characterize and compare their respective demographic niches. Demographic niches were compared to microsite characterization of treeless tundra substrates to understand what factors may constrain establishment. Then, in Chapter Three, I applied this demographic niche concept across a spatial gradient to assess changes in suitable microsite availability towards the range edge.

Specifically, I ask the following research questions:

Chapter Two:

- How does the niche space presently occupied by treeline black spruce individuals change throughout the life cycle in northern Yukon?
- If niche shifts occur, what microsite variables drive these niche shifts?
- What tundra conditions are negatively associated with black spruce colonization?

Chapter Three:

- How does suitable microsite availability change towards the range edge throughout black spruce's life cycle?
- How do viable seed availability and germination rates change towards the range edge?
- Which life stage(s) are the main demographic bottlenecks on range expansion?

This thesis informs which life stages are the limiting bottlenecks on northern black spruce range expansion. In turn, this will help us better understand the circumstances where treeline advance will likely occur under continued climate change. Studies often associate seedling occurrence beyond the range as evidence of advance (e.g., Harsch et al. 2009). Yet, if a niche contraction occurs and conditions are unsuitable for later life stages, individuals will die and the range will remain unchanged (Máliš et al. 2016). Furthermore, if the reproduction niche is narrower than the adult survival niche, range forecasts that primarily focus on adult presence could overestimate suitable niche space and predict range shifts in unsuitable areas for reproductive maturity, forming a non-reproductive sink population (Holt 2009; Schurr et al. 2012). Unless these sink populations continue to be maintained via dispersal from source populations, the population will go extinct (Pulliam 1988). Therefore, demographic niches provide valuable insights into how a species' distribution will respond to climate change. The approaches outlined in this thesis can be expanded spatially across a species' range to further understand demographic constraints on species' distributions and abundances.

1.7 References

Alexander, J. M., J. M. Diez, S. P. Hart, and J. M. Levine. 2016. When climate reshuffles competitors: A call for experimental macroecology. Trends in Ecology and Evolution 31:831–841.

Anderson, J. T., A. A. Landi, and P. L. Marks. 2009. Limited flooding tolerance of juveniles restricts the distribution of adults in an understory shrub *(Itea virginica; Iteaceae)*. American Journal of Botany 96:1603–1611.

Arieira, J., J. Penha, C. Nunes da Cunha, and E. Guimarães Couto. 2016. Ontogenetic shifts in habitat-association of tree species in a neotropical wetland. Plant Soil 404:219–236.

Batllori, E., J. J. Camarero, J. M. Ninot, and E. Gutiérrez. 2009. Seedling recruitment, survival and facilitation in alpine Pinus uncinata tree line ecotones. Implications and potential responses to climate warming. Global Ecology and Biogeography 18:460–472.

Bertrand, R., J.-C. Gégout, and J. Bontemps. 2011. Niches of temperate tree species converge towards nutrient-richer conditions over ontogeny. Oikos 120:1479–1488.

Black, R. A., and L. C. Bliss. 1980. Reproductive ecology of *Picea mariana* (Mill.) BSP., at tree line near Inuvik, Northwest Territories, Canada. Ecological Monographs 50:331–354.

Brodersen, C. R., M. J. Germino, D. M. Johnson, K. Reinhardt, W. K. Smith, L. M. Resler, M. Y. Bader, et al. 2019. Seedling survival at timberline is critical to conifer mountain forest elevation and extent. Frontiers in Forests and Global Change 2:1–12.

Brown, C. D., G. Dufour-Tremblay, R. G. Jameson, S. D. Mamet, A. J. Trant, X. J. Walker, S. Boudreau, et al. 2019. Reproduction as a bottleneck to treeline advance across the circumarctic forest tundra ecotone. Ecography 43:137–147.

Bykova, O., I. Chuine, X. Morin, and S. I. Higgins. 2012. Temperature dependence of the reproduction niche and its relevance for plant species distributions. Journal of Biogeography 39:2191–2200.

Chapin, F. S., M. Sturm, M. C. Serreze, J. P. McFadden, J. R. Key, A. H. Lloyd, A. D. McGuire, et al. 2005. Role of land-surface changes in arctic summer warming. Science 310:657–660.

Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chtamalus stellatus.* Ecology 42:710–723.

Cranston, B. H., and L. Hermanutz. 2013. Seed-seedling conflict in conifers as a result of plant-plant interactions at the forest-tundra ecotone. Plant Ecology and Diversity

6:319–327.

Davis, E. L., and Z. Gedalof. 2018. Limited prospects for future alpine treeline advance in the Canadian Rocky Mountains. Global Change Biology 24:4489–4504.

Donohue, K., R. Rubio de Casas, L. Burghardt, K. Kovach, and C. G. Willis. 2010. Germination, postgermination adaptation, and species ecological ranges. Annual Review of Ecology, Evolution, and Systematics 41:293–319.

Dufour-Tremblay, G., L. De Vriendt, E. Lévesque, and S. Boudreau. 2012. The importance of ecological constraints on the control of multi-species treeline dynamics in Eastern Nunavik, Québec. American Journal of Botany 99:1638–1646.

Eriksson, O. 2002. Ontogenetic niche shifts and their implications for recruitment in three clonal *Vaccinium shrubs: Vaccinium myrtillus, Vaccinium vitis-idaea,* and *Vaccinium oxycoccos.* Canadian Journal of Botany 80:635–641.

Fraser, J. W. 1976. Viability of Black Spruce Seed in or on a Boreal Forest Seedbed. The Forestry Chronicle 52:229–231.

Freeman, B. G., J. A. Lee-Yaw, J. M. Sunday, and A. L. Hargreaves. 2018. Expanding, shifting and shrinking: The impact of global warming on species' elevational distributions. Global Ecology and Biogeography 27:1268–1276.

Germino, M. J., W. K. Smith, and A. C. Resor. 2002. Conifer seedling distribution and survival in an alpine-treeline ecotone. Plant Ecology 162:157–168.

Ghosh, S., K. Zhu, A. E. Gelfand, and J. S. Clark. 2016. Joint modeling of climate niches for adult and juvenile trees. Journal of Agricultural, Biological, and Environmental Statistics 21:111–130.

Grace, J., F. Beringer, and L. Nagy. 2002. Impacts of climate change on the tree line. Annals of Botany 90:537–544.

Grinnell, J. 1917. The niche-relationships of the California Thrasher. The Auk 34:427–433.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: The importance of the regeneration niche. Biological Reviews 52:107–145.

Hargreaves, A. L., K. E. Samis, and C. G. Eckert. 2014. Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. The American Naturalist 183:157–173.

Harper, J. L. 1977. Population biology of plants. Academic Press Inc., London, U.K.

Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology Letters 12:1040–1049.

Hobbie, S. E., K. J. Nadelhoffer, and P. Högberg. 2002. A synthesis: The role of nutrients as constraints on carbon balances in boreal and arctic regions. Plant and Soil

242:163–170.

Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. Proceedings of the National Academy of Sciences 106:19659–19665.

Holtmeier, F. K. 2009. Mountain Timberlines: Ecology, Patchiness, and Dynamics. Springer, New York.

Holtmeier, F. K., and G. Broll. 2007. Treeline advance - driving processes and adverse factors. Landscape Online 1:1–33.

Hu, F. S., L. B. Brubaker, D. G. Gavin, P. E. Higuera, J. A. Lynch, T. S. Rupp, and W. Tinner. 2006. How climate and vegetation influence the fire regime of the alaska boreal biome: The holocene perspective. Mitigation and Adaptation Strategies for Global Change 11:829–846.

Humboldt, A. von, and A. Bonpland. 1807. Essay on the geography of plants. University of Chicago Press.

Hutchinson, G. E. 1957. Concluding Remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427.

Jameson, R. G., A. J. Trant, and L. Hermanutz. 2015. Insects can limit seed productivity at the treeline. Canadian Journal of Forest Research 45:286–296.

Johnston, W., and T. Smith. 1985. Black Spruce. Pages 96–98 *in* Silvicultural systems for the major forest types of the United States.

Kambo, D., and R. K. Danby. 2017. Constraints on treeline advance in a warming climate: A test of the reproduction limitation hypothesis. Journal of Plant Ecology 11:411–422.

Kasischke, E. S., D. L. Verbyla, T. S. Rupp, A. D. McGuire, K. A. Murphy, R. Jandt, J. L. Barnes, et al. 2010. Alaska’s changing fire regime — implications for the vulnerability of its boreal forests. Canadian Journal of Forest Research 40:1313–1324.

Körner, C. 1998. A re-assessment of high elevation treeline positions and their explanation. Oecologia 115:445–459.

Körner, C. 2012. Alpine treelines: Functional ecology of the global high elevation tree limits.

Krebs, C. J., J. M. LaMontagne, A. J. Kenney, and S. Boutin. 2012. Climatic determinants of white spruce cone crops in the boreal forest of southwestern Yukon. Botany 90:113–119.

Kroiss, S. J., and J. HilleRisLambers. 2015. Recruitment limitation of long-lived conifers: Implications for climate change responses. Ecology 96:1286–1297.

Lee-Yaw, J. A., H. M. Kharouba, M. Bontrager, C. Mahony, A. M. Csergo, A. M. E. Noreen, Q. Li, et al. 2016. A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. Ecology Letters 19:710–722.

Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. The velocity of climate change. Nature 462:1052–1055.

Maguire, B. 1973. Niche response structure and the analytical potentials of its relationship to the habitat. The American Naturalist 107:213–246.

Malcolm, J. R., A. Markhan, R. P. Neilson, and M. Garaci. 2002. Estimated migration rates under scenarios of global climate change. Journal of Biogeography 29:835–849.

Máliš, F., M. Kopecký, P. Petřík, J. Vladovič, J. Merganič, and T. Vida. 2016. Life stage, not climate change, explains observed tree range shifts. Global Change Biology 22:1904–1914.

McArthur, R. H. 1972. Geographical ecology: Patterns in the distribution of species. Harper and Row, New York, U.S.A.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MJM Software Design, Glenden Beach, Oregon U.S.A.

Parrish, J. A. D., and F. A. Bazzaz. 1985. Ontogenetic niche shifts in old-field annuals. Ecology 66:1296–1302.

Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? Global Ecology and Biogeography 12:361–371.

Pepin, N., R. S. Bradley, H. F. Diaz, M. Baraer, E. B. Caceres, N. Forsythe, H. Fowler, et al. 2015. Elevation-dependent warming in mountain regions of the world. Nature Climate Change 5:424–430.

Pérez-Ramos, O., I. R. Urbieta, M. A. Zavala, and T. Marañon. 2012. Ontogenetic conflicts and rank reversals in two Mediterranean oak species: Implications for coexistence. Journal of Ecology 100:467–477.

Pironon, S., J. Villellas, W. Thuiller, V. M. Eckhart, M. A. Geber, D. A. Moeller, and M. B. García. 2018. The "Hutchinsonian niche" as an assemblage of demographic niches: Implications for species geographic ranges. Ecography 41:1103–1113.

Pulliam, H. R. 2000. On the relationship between niche and distribution. Ecology Letters 3:349–361.

Pulliam, R. H. 1988. Sources, sinks, and population regulation. The American Naturalist 132:652–661.

Quero, J. L., L. Gómez-Aparico, R. Zamora, and F. T. Maestre. 2008. Shifts in the regeneration niche of an endangered tree *(Acer opalus ssp. granatense)* during ontogeny: Using an ecological concept for application. Basic and Applied Ecology 9:635–644.

Rannow, S. 2013. Do shifting forest limits in south-west Norway keep up with climate change? Scandanavian Journal of Forest Research 28:574–581.

Renard, S. M., E. J. B. McIntire, and A. Fajardo. 2016. Winter conditions - not summer temperature - influence establishment of seedlings at white spruce alpine treeline in Eastern Quebec. Journal of Vegetation Science 27:29–39.

Resler, L., D. Butler, and G. Malanson. 2005. Topographic shelter and conifer establishment and mortality in an alpine environment, Glacier National Park, Montana. Physical Geography 26:112–125.

Safford, L. O. 1974. Picea A. Dietr. Spruce. Pages 587–596 Seeds of woody plants in the United States. Washington, D.C.

Schupp, E. W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany 82:399–409.

Schurr, F. M., J. Pagel, J. S. Cabral, J. Groeneveld, O. Bykova, R. B. O'Hara, F. Hartig, et al. 2012. How to understand species' niches and range dynamics: A demographic research agenda for biogeography. Journal of Biogeography 39:2146–2162.

Smith, A. B., W. Godsoe, F. Rodríguez-Sánchez, H. Wang, and D. Warren. 2019. Niche estimation above and below the species level. Trends in Ecology & Evolution 34:260–273.

Stohlgren, T., R. Bachand, Y. Onami, and D. Blinkley. 1998. Species-environment relationships and vegetation patterns: Effects of spatial scale and tree life-stage. Plant Ecology 135:215–228.

Streicker, J. 2016. Yukon climate change indicators and key findings 2015. Northern Climate ExChange, Yukon Research Centre, Yukon College.

Sullivan, P. F., and B. Sveinbjörnsson. 2010. Microtopographic control of treeline advance in Noatak National Preserve, Northwest Alaska. Ecosystems 13:275–285.

Sveinbjörnsson, B., H. Kauhanen, and O. Nordell. 1996. Treeline ecology of mountain birch in the Torneträsk area. Ecological Bulletins 45:65–70.

Tarnocai, C., C. A. S. Smith, and C. A. Fox. 1993. International tour of permafrost affected soils: The Yukon and Northwest Territories of Canada. Ottawa.

Trant, A. J., R. G. Jameson, and L. Hermanutz. 2011. Persistence at the tree line: Old trees as opportunists. Arctic 64:367–370.

Wang, Y., N. Pederson, A. M. Ellison, H. L. Buckley, B. S. Case, E. Liang, and J. J. Camarero. 2016. Increased stem density and competition may diminish the positive effects of warming at alpine treeline. Ecology 97:1668–1679.

Wilson, C., J. Grace, S. Allen, and F. Slack. 1987. Temperature and stature: A study of temperatures in montane vegetation. Functional Ecology 1:405–413.

Zasada, J. C., T. L. Sharik, and M. Nygren. 1992. The reproductive process in boreal forests. Pages 95–135 *in* A systems analysis of the global boreal forest. Cambridge University Press, Cambridge, U.K.

Zuur, A. F., E. N. Ieno, and G. M. Smith. 2007. Analysing ecological data. Springer-Verlag New York.

Chapter 2: Integrating demographic niches shifts and northern black spruce range expansion

2.1 Abstract

When assessing the response of species' distributions to climate change, many studies estimate the niche at the species' level. However, species' niches can be examined demographically, allowing for the assessment of the unique dimensions representing demographic niches of different life stages. When a niche changes throughout the life cycle, it is known as an ontogenetic niche shift. While underused, this approach can identify demographic bottlenecks on climate-induced range expansion. We quantified microsites inhabited by four life stages of black spruce (*Picea mariana*) at subarctic treeline in Yukon to characterize demographic niches and assess how observed ontogenetic niche shifts may impact climate-induced changes in the distribution of this widespread boreal tree species. Microsite characteristics were compared to treeless tundra substrates to determine whether there are suitable microsites available for range expansion and to identify which factors limit establishment. Treelines in this region showed wide variation in tundra microsites available for establishment. Black spruce exhibited consecutive niche shifts and microsite associations from emergence to reproductive maturity, which were mainly driven by changes in plant community composition and soil moisture preferences. Overall, we found that (1) many black spruce seedlings at the range edge occupy unsuitable conditions for transitioning to the next life stage; and (2) reproductive adults have a narrow niche, limiting seed production to where suitable niche space is restricted. Together, our findings suggest that demographic niches

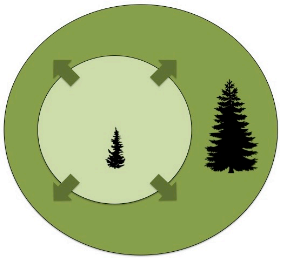
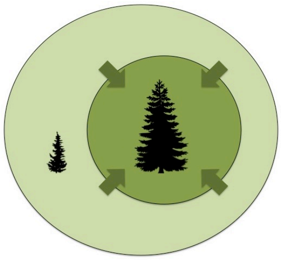
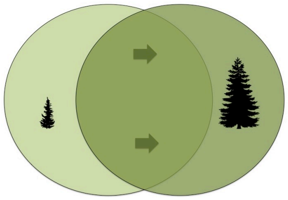
can highlight key hurdles to range expansion, providing a better understanding of how species' distributions will respond to climate change.

2.2 Introduction

Ecological niche theory has been fundamental for understanding species' abundances and distributions, and how those may respond to ongoing climate change. Species' niche limits often align with their range limits (Hargreaves et al. 2014; Lee-Yaw et al. 2016). A niche in this context refers to the Hutchinson niche defined as the n-dimensional hypervolume that sets the range of ecological conditions individuals can occur within (Hutchinson 1957). Although dispersal limitations and negative biotic interactions may prevent a species from occupying a suitable location (Pulliam 2000), species require suitable niche space to maintain reproductive populations, a key process in range expansion.

Many studies exploring the relationship between species' niches and distributions in a changing climate estimate the niche at the species level (Peterson et al. 2011; Smith et al. 2019). Yet, the Hutchinson niche can be divided demographically, where different life stages have unique hypervolumes forming multiple demographic niches (Maquire 1973; Grubb 1977; Pironon et al. 2018). The assemblage of demographic niches results in changing niche breadth throughout the life cycle and is known as an ontogenetic niche shift (Parrish and Bazzaz 1985). Ontogenetic niche shifts have been widely explored in animal ecology (e.g., Olson 1996; Hou et al. 2008), but remain less understood in plant species (but see Miriti 2006; Bertrand et al. 2011). Although plants cannot actively seek new habitat, they can respond in different ways to changes in environmental variables throughout their life history (Quero et al. 2008; Anderson et al. 2009). Depending on demographic niche composition, the range of ecological conditions that individuals can occupy can expand, contract, and directionally shift throughout its life history (Table 2.1). Demographic niches further refine the relationship between a species' niche and its geographic distribution where individuals can only exist within suitable niche space for their respective life stage.

Table 2.1 Different types of ontogenetic niche shifts and their implications on plant species' distributions. Images represent a two-dimensional depiction of a Hutchinson niche separated into demographic niches. The light and dark circles respectively represent the niche breadth of an early and late life stage. Arrows indicate the transition between life stages and an ontogenetic niche shift.

	Niche Expansion	**Niche Contraction**	**Directional Niche Shift**
Description	Earlier stages have stricter requirements than later stages 	Requirements are stricter at later stages than earlier stages 	Partially non-overlapping requirements across life stages 
Effects on species' ranges and abundance	Establishment restricted to a subset of conditions that later life stages could otherwise occupy	Wide spread mortality as individuals pass to the later stage or low seed availability if limited by the reproduction niche	Maladaptations and mortality of individuals as they transition to the later life stage
Examples	*Itea virginica* seedlings grew best on unflooded soil while adults tolerated a wide range of flooding (Anderson et al. 2009) *Triadica sebifera* germination occurred on a much stricter range of soil moisture conditions that other life stages could occupy (Gabler and Siemann 2013)	Adult *Vaccinium oxycoccos* only found close to wetlands while juveniles occupied a wider variety of habitats (Eriksson 2002) *Acer opalus* germinated in all available microsites while old saplings preferred shrub canopy with increased access to light (Quero et al. 2008)	Emergents preferred open areas whereas seedlings preferred dense micro-habitats for two *Quercus* species (Pérez-Ramos et al. 2012) Optimal germination on scarified substrates while optimal seedling growth on undisturbed soils for *Pinus nigra* (Lucas-Borja et al. 2012)

Considering demographic niches can strengthen our understanding of species' distributions (Pironon et al. 2018). Source-sink dynamics create discrepancies between niche limits and range limits where non-reproductive sink populations occupy unsuitable niche space (Pulliam 2000). Demographic niches can reconcile these discrepancies, where a sink population occurs when a species has a narrower reproduction niche than adult survival niche and reproduction niche space is absent in a given area. Using demographic niches in species' distribution models can separate sink populations from reproductive populations, and prevent forecasts from overestimating suitable area for that species (Holt 2009; Schurr et al. 2012). Additionally, the presence of early life stages beyond the range is often considered to indicate a range expansion (Máliš et al. 2016). Yet, if the species exhibits a niche contraction (Table 2.1) and conditions beyond the range are unsuitable for later life stages, maturing individuals will die and the range will remain unchanged (Máliš et al. 2016). By understanding demographic niche composition, we can better predict the circumstances where the presence of earlier life stages indicates a range expansion is occurring.

The influence demographic niches have on species' distributions can, in turn, impact its response to climate change if the species' sensitivity to climatic factors varies across life stages (Ettinger and HilleRisLambers 2013; Müller et al. 2018), particularly in northern latitudes which are experiencing intense climate warming (Chapin et al. 2005; Johannessen et al. 2016). As a result, northern regions are exhibiting major landscape changes involving increased forest fires, permafrost thaw, and species' range shifts (Streicker 2016). This rapidly changing region creates an excellent model system to understand demographic niches and their role in influencing species' distributions. High latitude forest-tundra ecotones (henceforth treelines) represent the northern limit of the boreal forest. Currently, 52% of treelines are estimated to be tracking their climatic niche northward to higher elevations or latitudes (Harsch et al. 2009). Although temperature may be suitable for tree establishment in the tundra ecosystem beyond the treeline, many other non-climatic factors can create unsuitable niche space for establishment (e.g., Smith et al. 2003; Wheeler et al. 2011). Boreal tree range expansion potential is further complicated if local tree species undergo niche shifts and respond to their environment in different ways throughout their life history.

The role of demographic niches in boreal tree range expansion remains unclear; however, all three ontogenetic niche shifts types (Table 2.1) have been identified in treeline taxa. Black spruce (*Picea mariana*) seedlings were found to be more sensitive to water stress than adults, suggesting an ontogenetic niche expansion (Black and Bliss 1980). Directional ontogenetic niche shifts can occur during seedling establishment and growth, where neighbouring plants create sheltered microsites to facilitate establishment but, as the seedling grows, this role shifts to detrimental resource competition (Lucas-Borja et al. 2012; Cranston and Hermanutz 2013). Ontogenetic niche contractions post-germination have been identified in the Swiss Alps (Hättenschwiler and Körner 1995). Additionally, northern conifer populations often have limited seed production (Sveinbjörnsson et al. 1996; Brown et al. 2019), indicating a niche contraction from adult survival to reproduction.

Although species' distributional changes of biogeographical interest occur on a large scale, the niche space that an individual directly experiences happens at a much finer scale. At this scale, regions are heterogeneous, creating a wide variety of microsites that may or may not be suitable for establishment. By comparing this fine scale variability to a species' demographic niches, we can identify the specific microsite conditions the species can inhabit. In this study, we asked: (1) How does the niche space presently occupied by treeline black spruce individuals change throughout the life cycle in northern Yukon? (2) If niche shifts occur, what microsite variables drive these niche shifts? And (3) What tundra conditions are negatively associated with black spruce colonization? Northern black spruce populations represent an excellent species to study niche shifts because seeds are wind dispersed, resulting in a wide spatial distribution of seeds.

Since trees have a long life span, it is difficult to follow an individual throughout its entire life. To overcome this, we compared the microsites inhabited by individuals of different life stages in a single growing season (as described by Quero et al. 2008). The Yukon is a fire prone landscape, with a fire return interval of ~80 - 150 years (Hu et al. 2006; Kasischke et al. 2010). This results in temporally changing available niche space, where fire periodically alters the understory by removing the plant community and organic layer which then both regenerate over time. Here, we assess demographic niches in undisturbed regions and infer post-fire demographic niche space for emergence from the literature (e.g., Hesketh et al. 2009; Veilleux-Nolin and Payette 2012; Brown et al. 2015). We selected sites that had not burned for at least 70 years (Government of Yukon 2017) with a variety of age classes, indicating recruitment occurred within undisturbed conditions for all but the oldest adults. To address our questions, we characterized demographic niches for four life stages of black spruce: emergents (recently germinated and <1-year-old), seedlings (≤60 cm tall), non-reproductive adults (>60 cm tall without cones), and reproductive adults (>60 cm tall with cones). Due to harsh growing conditions, northern black spruce populations often exhibit stunted growth forms (krummholz) that can be reproductively mature despite their small stature (<2 m); therefore, we considered any individual >60 cm an adult. Treeline ecotones are characterized by tundra substrate with decreasing tree density. Throughout the treeline, we also characterized microsites for "treeless tundra" in which no tree was present. This approach allowed us to assess the suitability of tundra substrates for black spruce colonization. Ultimately, our research will fill a fundamental gap in our understanding of the role a species' life history plays in climate induced range expansion.

2.3 Materials and Methods

2.3.1 Study area and species description

To capture the widest range of microsite conditions possible, we selected three black spruce dominated treeline sites near Eagle Plains, Yukon (66° 22' 12" N, 136° 43' 48" W) that were characterized by gradually decreasing tree density and having all life stages present (Fig. 2.1; Table 2.2). The region has continuous permafrost with a seasonal thaw depth of less than 1 m (Tarnocai et al. 1993). This area experiences a continental climate with a mean annual temperature from 1981-2010 of -8.3°C (Environment Canada 2019). Annual mean precipitation during this period was 278.6 mm (Environment Canada 2019).

Site One had a high lichen cover (primarily *Cladonia spp.*) with an understory shrub community primarily consisting of *Betula spp., Salix spp., Rhododendron spp., Vaccinium uliginosum, Empetrum nigrum,* and *Vaccinium visis-idaea*, and was interlaid with frost boils from freeze-thaw permafrost cycles. Sites Two and Three had a similar shrub community to Site One and were moss dominated (primarily *Sphagnum spp.* and *Hylocomium* spp.)

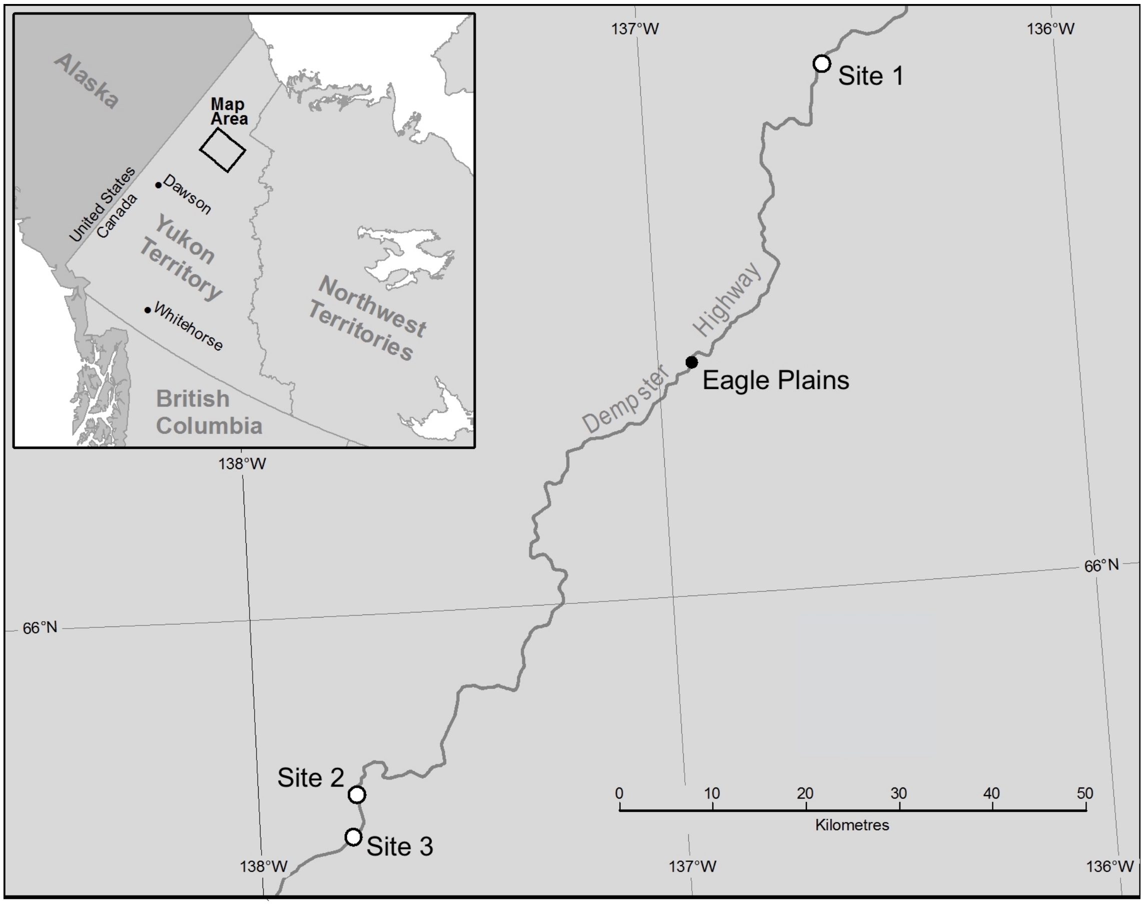


Figure 2.1 A map of our study region in northern Yukon, Canada. Map produced by David Mercer, Memorial University Libraries.

Table 2.2 A description of the three studies sites included in this study. Site age estimated via ground level tree cores. Note: basal diameter for trees at Site Three were too narrow to core any trees.

Site	**Location**	**Aspect (°)**	**Slope (°)**	**Stand Density (Trees/Ha)**	**Mean Adult Age (yrs)**	**Max Adult Age (yrs)**
One	66.491, -136.573	80	5	158	53.6	163
Two	65.855, -137.710	45	7	490	56.2	99
Three	65.784, -137.783	296	7	215	N/A	N/A

Black spruce is a long-lived semi-serotinous coniferous tree species commonly found on wet organic soils across the boreal forests of North America (Johnston and Smith 1985). Populations in the study region begin producing cones when 25-30 years old, and reliably produce cones at 85 years (Black and Bliss 1980). Black spruce retains several cone cohorts in an aerial seed bank and gradually releases seeds in the absence of fire (Zasada et al. 1992). If a stand is experiencing a low reproduction year, cones from previous years will still be present, and our classification of reproductive adults included trees that had successfully produced cones in previous years. Seed production is required for a landscape scale range shift to occur (Malcolm et al. 2002), however, black spruce exhibits vegetative reproduction by layering: forming adventitious roots on lateral branches to produce clonal stems. Black spruce seeds are dispersed by wind and known to travel up to 80 m from the windward edge of a mature stand (Johnston and Smith 1985). Once dispersed, seed loses its viability within 10 - 16 months (Fraser 1976).

2.3.2 Quantifying black spruce's demographic niches

Within each of the three sites, we established four 100 m x 10 m belt transects ~20 m apart and perpendicular to the treeline, heading towards the range edge (see Supplementary Fig. 2.1 for a diagram of study design). To select individuals close to the range edge, the zero marker for each transect indicated the last reproductive adult along the centre line of the transect. From this point, the transect extended 45 m towards the tundra and 55 m towards the forest. To capture the range of conditions each stage occupied at the northern limit, up to two each of seedlings, non-reproductive adults, reproductive adults, and treeless tundra substrates (measuring 50 cm x 50 cm) were randomly selected for demographic niche characterization every 10 m along the transect. We made note of any individuals that exhibited physical damage (e.g., substantial needle loss, brown needles). To quantify the niche for emergents, we seeded 50 cm x 50 cm experimental plots in 10 m increments along each transect at Sites One and Two. Site Three was not included in the seeding experiment due to an insufficient number of seeds. One hundred black spruce seeds were added to one seed plot while an adjacent plot acted as a non-seeded control for a total of 80 control and 80 seed plots. Seeds used for the seeding experiment were collected in Clear Creek, Yukon (63° 42' N, 137° 40' W) and stored at the National Tree Seed Centre (Fredericton, NB; NTSC number: 9570031). The NTSC laboratory germination rate was 80.5%. The seeding experiment was established at Site One in July 2017. No emergence had occurred when plots were surveyed in June 2018. Plots at both sites were seeded in June 2018 and emergence was recorded in August 2018.

The microsite each stage inhabited was defined as the 50 cm x 50 cm seed plot for the emergent niche, the area within 25 cm of tree base for remaining individuals, and a 50 cm x 50 cm quadrat for treeless tundra. To characterize each demographic niche, we recorded the following variables at each microsite: active layer depth, organic layer depth, soil moisture, soil temperature, soil pH, light availability, microtopography, and plant community composition. Active layer depth was measured with a frost probe as the depth to permafrost or rock in peak growing season (July 2018). Organic layer depth was determined as the distance from the mineral soil to the base of the vegetation layer. Soil moisture was measured with a decagon GS3 Ruggedized Soil Moisture Sensor on a dry summer day. Soil temperature was measured twice during the growing season with a Hanna Instruments soil conductivity and temperature meter on two separate days. Soil temperature and moisture measurements were collected for all microsites within a site on the same day. For soil pH, 15 g of soil was collected and mixed with 15 mL of distilled water. The mixture was stirred and left for 30 min to form a slurry (Robertson et al. 1999). The pH of the slurry was then measured with a Hanna Instruments pHep pocket-sized pH meter. Light availability represents the proportion of light an individual receives relative to ambient air, measured with Extech HD450 datalogging light meter. For microtopography, we noted whether the individual was growing on a flat surface, hummock, or hollow but found that almost all microsites (96%) were flat surface and the variable was not used in analyses. For plant community composition, we noted the percent composition within the microsite of the following functional groups: moss, lichen, forbs, graminoids, and shrubs. Shrubs were recorded to species level and then grouped into three categories based on the functional height of the species: tall shrubs (e.g., *Betula glandulosa, Salix glauca.)*, medium shrubs (e.g., *Rhododendron spp., Vaccinium uliginosum)*, and dwarf shrubs (e.g., *Empetrum nigrum, Vaccinium visis-idaea, Arcostaphylos uva-ursi)*. For the emergent niche, we noted the functional group the individual germinated on within the seed plot.

2.3.3 Data analysis

We performed non-metric multidimensional scaling (NMDS) to quantify black spruce's demographic niches using the vegan package version 2.5.2 (Oksanen et al. 2013) in the R environment (R Core Team 2019). NMDS is a non-parametric ordination method that is well suited to ecological data that violate parametric ordination assumptions (McCune and Grace 2002). We used Gower distances to calculate distance matrices as it works well for datasets with mixed variables (i.e., plant cover and environmental variables; Legendre and Legendre 2012). We ran the analysis with one to six dimensions and selected the model that minimized both stress and dimensions (McCune and Grace 2002). An NMDS to compare life stages was made for each of the three sites and all sites combined. For the model combining all sites, variables were standardized to the site mean and standard deviation to analyze differences between where individuals were growing relative to what was present at the site. This allowed for comparison between sites that may experience different site-specific factors (e.g., one site may be in a wetter region but still experience the same relative niche shifts). If the NMDS included the emergent niche, functional group variables were not included as the substrate the emergent germinated on was at a much smaller scale (i.e., <1 cm x 1 cm) than the scale the functional groups were assessed at (i.e., 50 cm x 50 cm). Light availability was also not included if the NMDS included the emergent niche due to equipment failure. Otherwise, all microsite variables were included in NMDS analyses. Ninety-five percent confidence interval ellipses were created around the centroid of each life stage to show each demographic niche. We identified microsite preferences for a given life stage with the ordiareatest function in the vegan package, which determined if a group was more tightly clustered than expected by chance (Oksanen et al. 2013).

To assess the influence of each microsite variable in driving observed niche shifts, we used general linear mixed models (GLMMs) with a Gaussian distribution from the "lme4" package version 1.1-21 (Bates et al. 2015). For each model, the microsite variable was the response variable with life stage as the explanatory variable and transect nested within site as random effects. If the GLMM violated model assumptions, the statistical decision was confirmed using a randomization test with 5000 permutations (Manley 2006). F-statistics from 5000 GLMMs modelled with samples of the response variable were calculated to obtain an assumption-free empirical distribution. The probability of the F-statistics obtained from the original GLMM was then determined using this empirical distribution. We performed Tukey honest significant difference (HSD) post-hoc tests to identify differences in microsite variables between life stages.

2.4 Results

In total, we characterized the microsites of 165 seedlings, 97 non-reproductive adults, 122 reproductive adults, and 240 treeless tundra substrates (see Supplementary Fig. 2.2 and Table 2.1 for site breakdown of sample size). Due to logistical constraints associated with remote field work, sample sizes differed slightly between microsite parameters. We only included individuals with all microsite variables for NMDS analyses, resulting in 157 seedlings, 94 non-reproductive adults, 120 reproductive adults, and 215 treeless tundra substrates. Emergence of black spruce at seed addition plots was very low with emergents present at 4/40 and 14/40 seed addition plots at Sites One and Two, respectively (overall germination success rate of 0.113% and 3.125% at Sites One and Two, respectively). To avoid pseudo-replication, the sample unit used for the emergent niche was a seed plot; if multiple emergents were present in a seed plot they were considered to be growing in the same niche space. The emergent niche was only included in analyses for Site Two as it was the only site with a sufficient sample size.

2.4.1 Demographic niche shifts

NMDS ordinations revealed shifting demographic niche breadth and microsite associations throughout the life cycle (Fig. 2.2, 2.3). All ordinations produced an acceptable fit (stress ≤ 0.178; Clarke 1993) in four and three dimensions for the ordination with all sites and site-specific ordinations, respectively. In ordination space, individuals that are closer together have more similar microsite characteristics than those that are farther apart. For all ordinations, treeless tundra substrates were widely distributed across ordination space demonstrating the variety of microsites available.

At Site Two, the only site with sufficient germination for our analysis, the emergent niche was narrow relative to other life stages. Emergents occupied a limited subset of available treeless tundra substrates and were more tightly clustered than expected by chance (p = 0.077), suggesting strict microsite preferences for this life stage (orange ellipse; Fig. 2.3). Seedlings had the broadest niche of all life stages but were tightly clustered (green ellipses; Fig. 2.2, 2.3; ordination of all sites p = 0.06; Site One p = 0.002; Site Two p = 0.09; Site Three p = 0.001) indicating microsite preferences within the total environment. Transitioning from seedlings to non-reproductive adults, directional niche shifts occurred at all sites with partially non-overlapping 95% confidence ellipses (green to purple ellipses; Fig. 2.2, 2.3). When all sites were ordinated together, a niche contraction from seedlings to non-reproductive adults occurred with many seedlings on the periphery of their niche exhibiting physical damage (e.g., browning needles or substantial needle loss; Fig. 2.2, 2.3). The ordination combining all three sites exhibited a niche contraction from non-reproductive to reproductive adults (purple to blue ellipses), where reproductive adults were tightly clustered (p = 0.001; Fig. 2.2, 2.3) suggesting strong microsite associations compared to the total environment.

Site-specific patterns were observed between adult groups. Sites One and Three exhibited a directional niche expansion and Site Two exhibited a niche contraction from non-reproductive adults to reproductive adults (Fig. 2.3). All sites except Site Two had adults occupying exclusive ordination space that no treeless tundra points were present within where adults likely created novel microsite characteristics that differ from the treeless tundra environment (Fig. 2.2, 2.3).

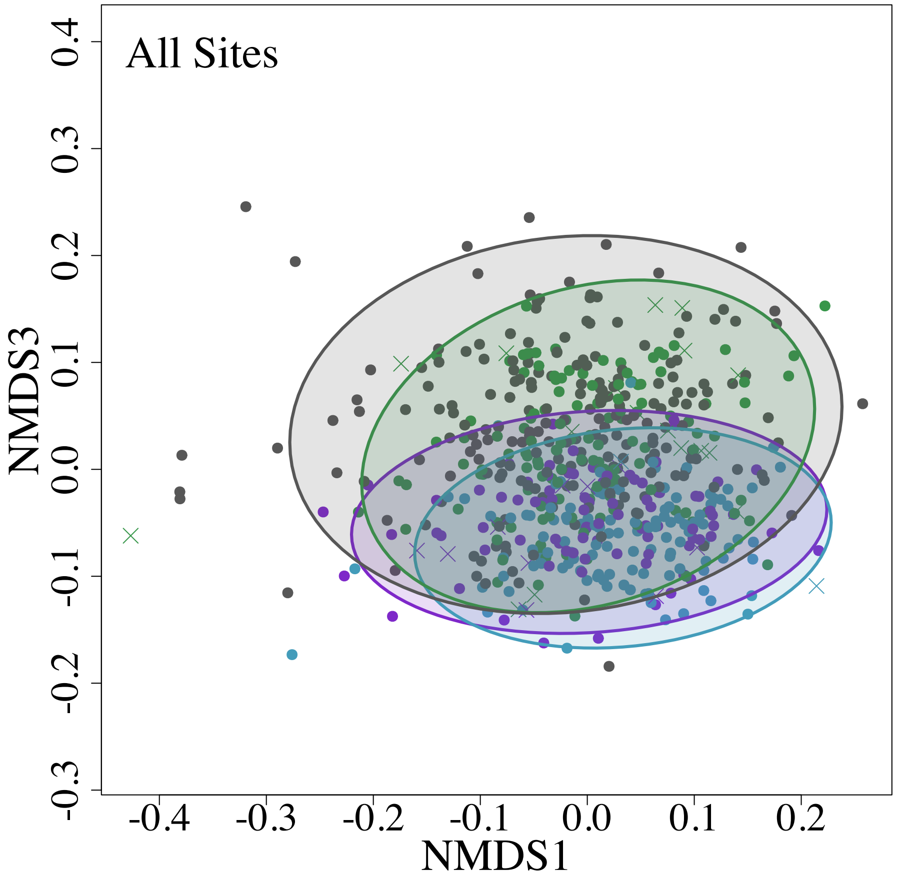


Figure 2.2 NMDS ordination of black spruce's demographic niches for all three sites combined (stress = 0.159 in 4 dimensions). NMDS axes that most substantially display niche shifts are shown. Points represent an individual or treeless tundra substrate in ordination space (seedlings = green, non-reproductive adults = purple, reproductive adults = blue, and treeless tundra = gray). Shapes signify health, where X = an unhealthy individual of any life stage and circle = an individual of normal health or treeless tundra substrate. Ellipses are 95% confidence intervals around the centroids of each life stage, representing each demographic niche in ordination space.

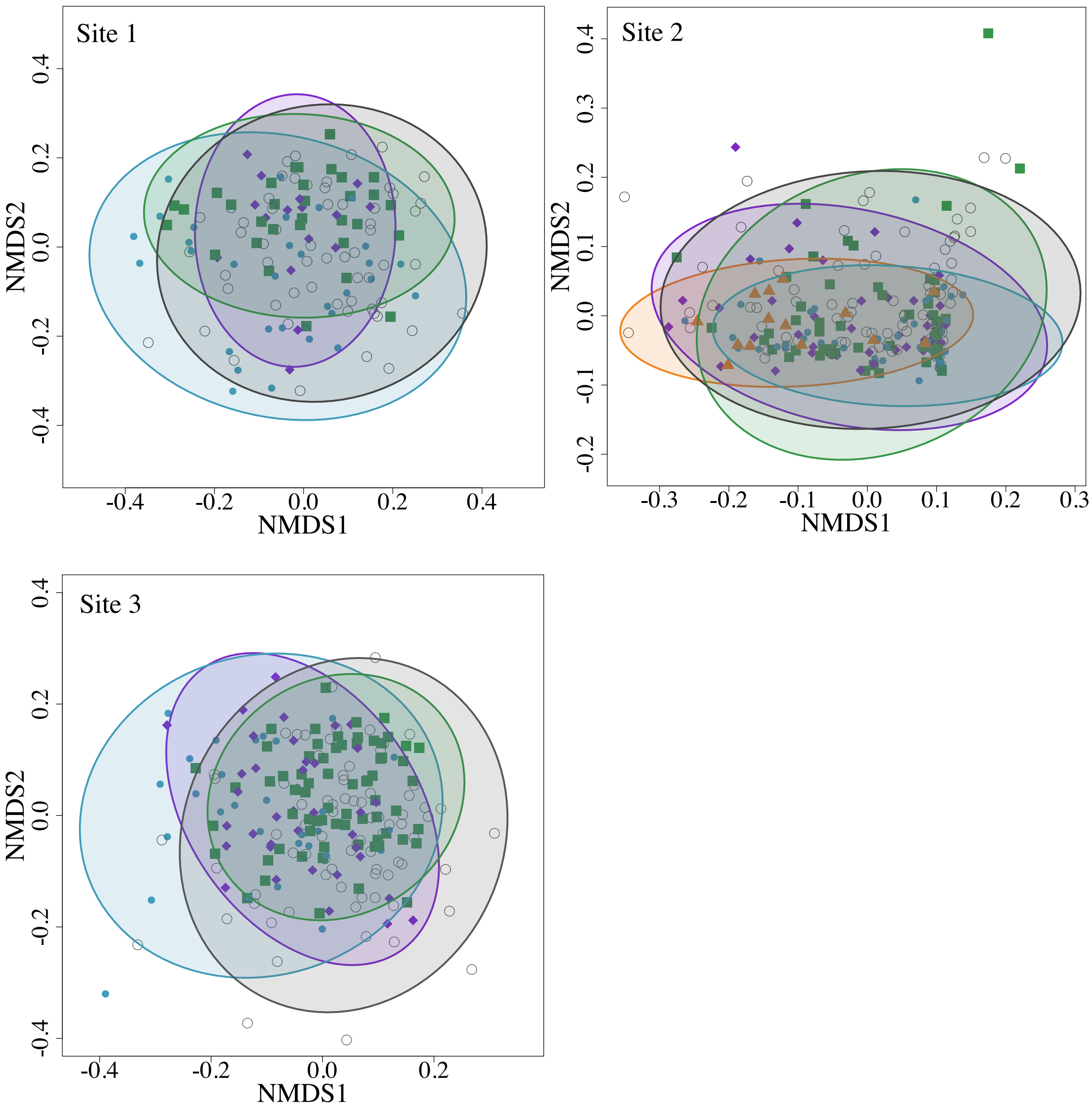
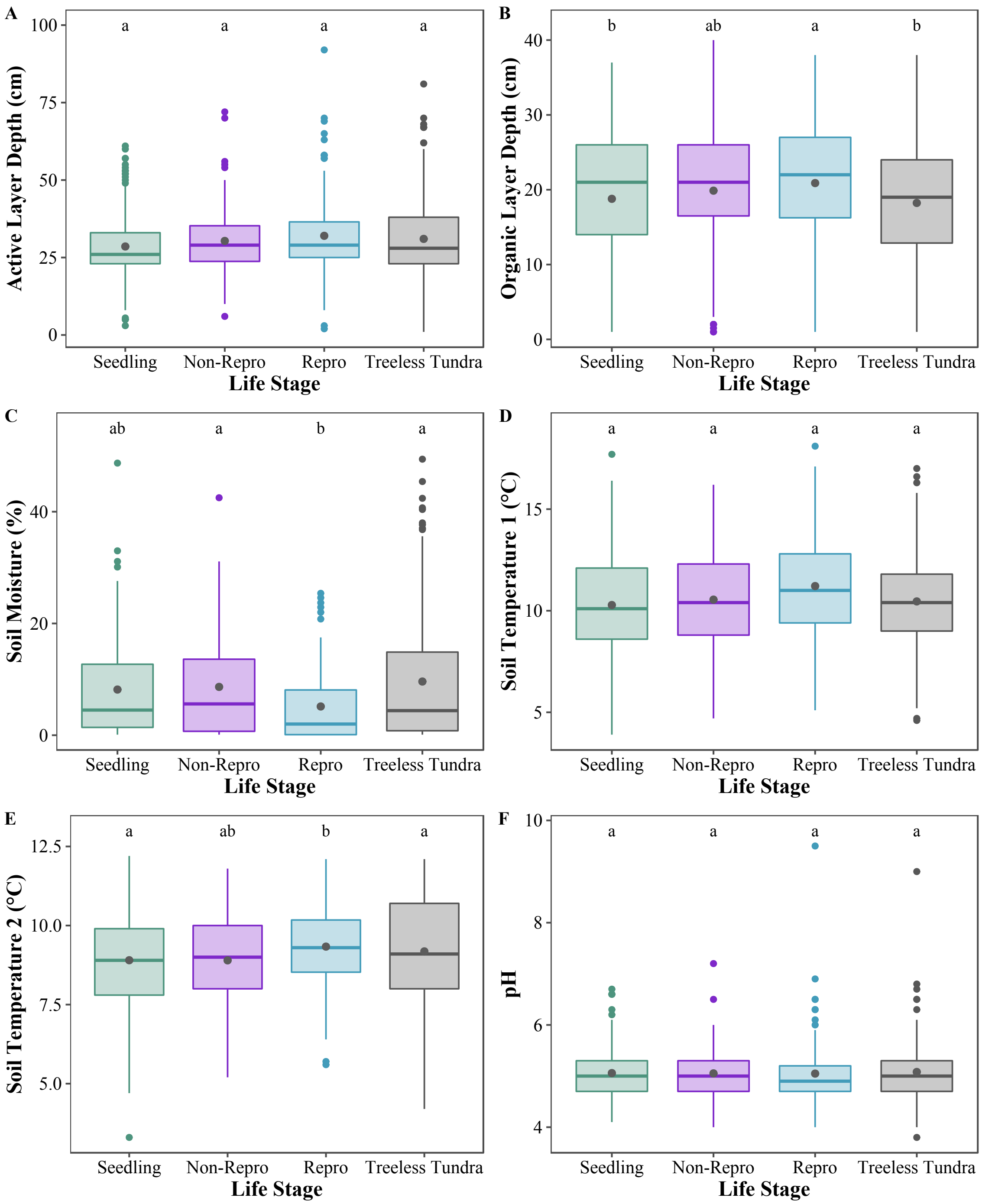


Figure 2.3 NMDS ordinations of black spruce's demographic niches for Site One (stress = 0.174 in 3 dimensions); Site Two (stress = 0.081 in 3 dimensions); and Site Three (stress = 0.178 in 3 dimensions). NMDS axes that most substantially display niche shifts for each ordination are shown. Points represent an individual or treeless tundra substrate in ordination space (emergent = orange triangles, seedlings = green squares, non-reproductive adults = purple diamonds, reproductive adults = blue full circles, and

treeless tundra = gray hollow circles). Shapes correspond to the life stages. Ellipses are 95% confidence intervals around the centroids of each life stage, representing each demographic niche in ordination space.

2.4.2 Microsite characteristics driving niche shifts

GLMMs and Tukey HSD post hoc tests identified many small but statistically significant differences in microsite variables between life stages (Fig. 2.4; Table 2.3, supplementary Table 2.2). Treeless tundra substrates tended to have more tall shrubs and lichen dominated ground cover than microsites with trees (Fig. 2.4). One hundred percent of emergents at Site Two germinated exclusively on moss substrates and were present in moister soils than other stages ($F_{4,244} = 3.3301$, $p = 0.01$). Seedlings received more light and were present within a lower graminoid cover than treeless tundra substrates (Fig. 2.4). Seedlings and non-reproductive adults occupied microsites with a higher cover of dwarf shrubs than other stages (Fig. 2.4J). Compared to all other life stages, reproductive adults were found on drier, warmer soils, with deeper organic layers, with fewer shrubs, and more moss cover (Fig. 2.4). There were no significant differences in active layer depth or pH between any life stages (Fig. 2.4). Randomization tests performed on GLMMs violating model assumptions did not change the statistical decision at the 0.05 level.


A
Active Layer Depth (cm)
100
75
50
25
0
a
a
a
a
Seedling
Non-Repro
Repro
Treeless Tundra
Life Stage
B
Organic Layer Depth (cm)
40
30
20
10
0
b
ab
a
b
Seedling
Non-Repro
Repro
Treeless Tundra
Life Stage
C
Soil Moisture (%)
40
20
0
ab
a
b
a
Seedling
Non-Repro
Repro
Treeless Tundra
Life Stage
D
Soil Temperature 1 (°C)
15
10
5
a
a
a
a
Seedling
Non-Repro
Repro
Treeless Tundra
Life Stage
E
Soil Temperature 2 (°C)
12.5
10.0
7.5
5.0
a
ab
b
a
Seedling
Non-Repro
Repro
Treeless Tundra
Life Stage
F
pH
10
8
6
4
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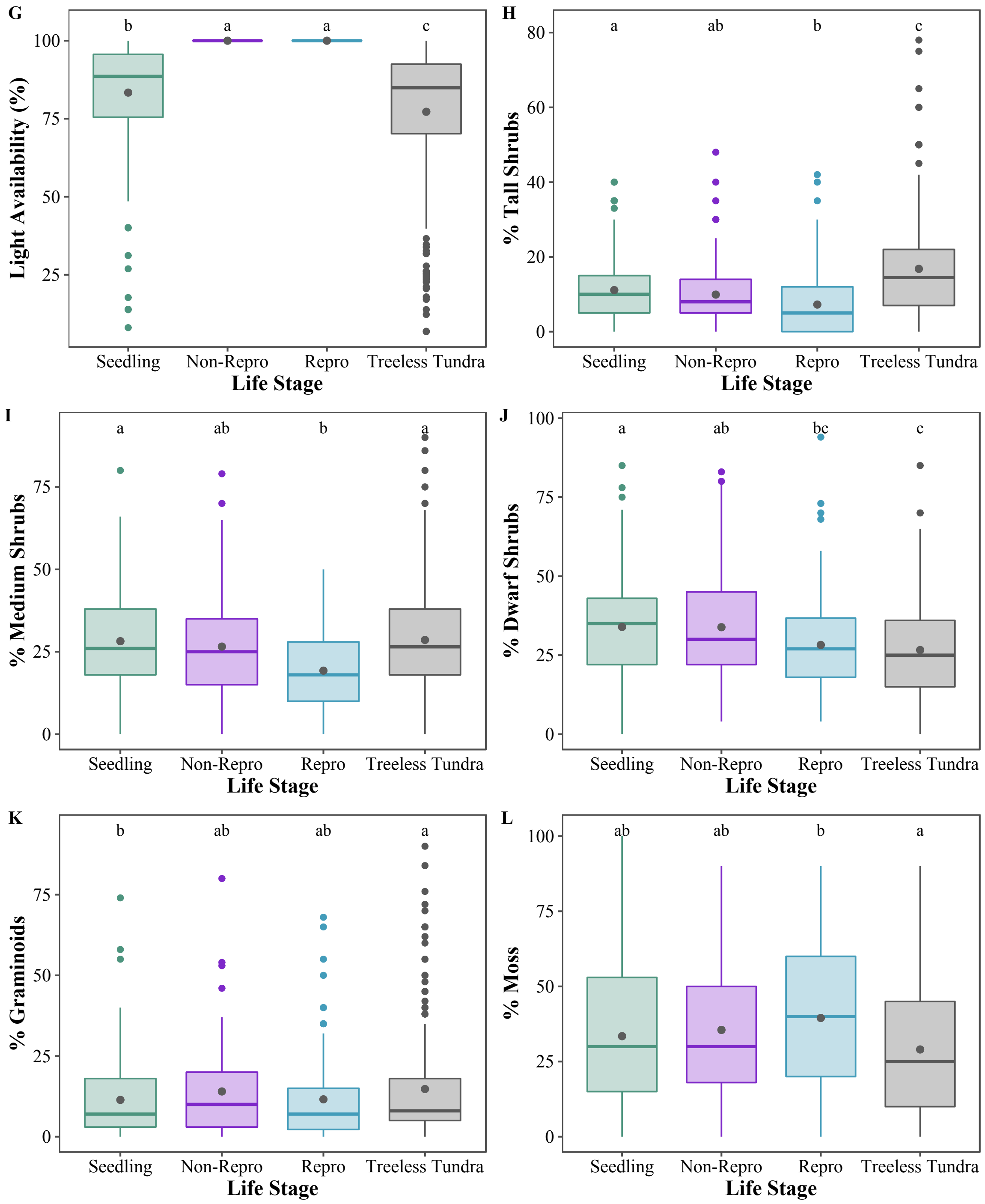
Seedling
Non-Repro
Repro
Treeless Tundra
Life Stage


G
Light Availability (%)
100
75
50
25
b
a
a
c
Seedling
Non-Repro
Repro
Treeless Tundra
Life Stage
H
% Tall Shrubs
80
60
40
20
0
a
ab
b
c
Seedling
Non-Repro
Repro
Treeless Tundra
Life Stage
I
% Medium Shrubs
75
50
25
0
a
ab
b
a
Seedling
Non-Repro
Repro
Treeless Tundra
Life Stage
J
% Dwarf Shrubs
100
75
50
25
0
a
ab
bc
c
Seedling
Non-Repro
Repro
Treeless Tundra
Life Stage
K
% Graminoids
75
50
25
0
b
ab
ab
a
Seedling
Non-Repro
Repro
Treeless Tundra
Life Stage
L
% Moss
100
75
50
25
0
ab
ab
b
a
Seedling
Non-Repro
Repro
Treeless Tundra
Life Stage

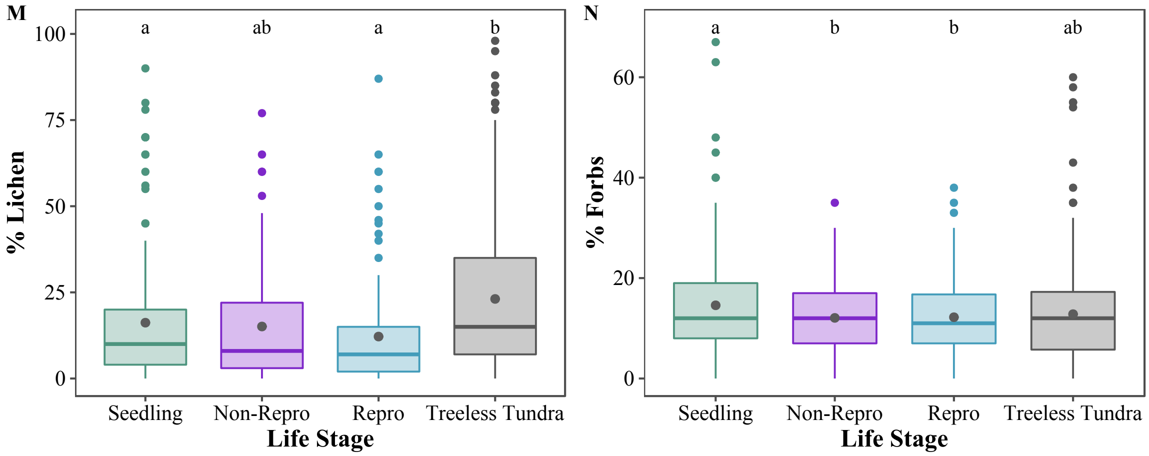


Figure 2.4 Boxplots depicting microsite conditions occupied by different black spruce life stages at all three sites for (A.) frost depth; (B.) organic layer depth; (C.) soil moisture; (D.) soil temperature 1; (E.) soil temperature 2 measured on a separate day; (F.) pH; (G.) relative light availability; (H.) % cover tall shrubs; (I.) % cover medium shrubs; (J.) % cover dwarf shrubs; (K) % cover graminoids; (L.) % cover moss; (M.) % cover lichen; and (N.) % cover forbs. The emergent niche is not shown as sufficient germination was only present at one site. The line in the centre of the boxes is the median of that stage and the grey point is the mean. The boxes encompass the 25%–75% quartiles. The whiskers extending beyond the boxes represent the 95% quartiles, and extreme observations are points beyond the whiskers. Letters above boxes indicate significant differences between groups. Results of GLMMs summarized in Table 2.3.

Table 2.3 Summary of GLMMs for Figure 2.4 comparing microsite variables between black spruce life stages with transect nested within site as a random factor (values not shown). P-value is for the entire model. The emergent niche is not included in this model set as sufficient germination was only present at one site; results are reported in text. Bold indicates p-values that are significant at the 0.05 level for the GLMM model. N indicates the sample size for the GLMM which varied slightly between variables due to logistical constraints. * indicates revised p-value from randomization test performed due to model assumption violations, no revised p-values change significant decision at the 0.05 level.

Response Variable	n	F-Value	P value
Active Layer Depth (cm)	622	1.7145	0.1718*
Soil Organic Layer Depth (cm)	623	**3.6285**	**0.0129**
Soil Moisture (%)	623	**4.4637**	**0.0052***
Soil Temperature 1 (°C)	623	2.3886	0.0678
Soil Temperature 2 (°C)	624	**3.3688**	**0.0204***
pH	622	0.2100	0.8895
Relative Light Availability	590	**83.270**	**<0.0001***
Tall Shrubs (% Cover)	624	**23.853**	**<0.0001***
Medium Shrubs (% Cover)	624	**11.856**	**<0.0001**
Dwarf Shrubs (% Cover)	624	**8.4593**	**<0.0001**
Graminoids (% Cover)	624	**2.8595**	**0.0370***
Moss (% Cover)	624	**3.8108**	**0.0100**
Lichen (% Cover)	624	**8.2798**	**<0.0001***
Forbs (% Cover)	624	**4.2477**	**<0.0001***

2.5 Discussion

Black spruce's niche shifts throughout its life cycle, with microsite associations changing from emerging seedling to reproductively mature adult (Fig. 2.5). We found black spruce had a narrow emergent niche that expanded to a broad seedling niche. While available niche space for adults differed between sites, overall, adult groups had narrow niche breadths, with reproductive adults having a particularly narrow niche. Similar niche contractions, with narrowing microsite associations during the life span, have been observed in Scandinavian *Vaccinium* spp. (Eriksson 2002), *Acer opalus* in Spain (Quero et al. 2008), and several temperate European tree species (Bertrand et al. 2011). While these trends may be partly related to adults altering their own microsite over time, niche contractions can lead to widespread mortality of individuals during the transition to later life stages if suitable conditions are not present. Indeed, several seedlings growing at the periphery of the seedling niche were unhealthy (e.g., brown needles, substantial needle loss) suggesting they may have found themselves growing in unsuitable conditions for the transition to the next life stage. Overall, we provide empirical evidence that many seedlings at the range edge occupy unsuitable conditions for adult establishment and that black spruce's narrow reproduction niche will limit seed production in the absence of suitable conditions.

The emergent niche is the initial bottleneck for a dispersed seed to colonize novel habitat. Germination was very low in our seeding experiment, with successful emergence occurring in a narrow range of conditions. This narrow emergent niche was driven by a preference for wetter substrates and high moss cover, specifically *Sphagnum spp.* and feathermoss, similar to black spruce emergence observed across its geographic distribution (Wheeler et al. 2011; Veilleux-Nolin and Payette 2012; Brown et al. 2015). Low emergence could also be attributed to seed predation which can impede establishment (Munier et al. 2010; Kambo and Danby 2017) and may vary spatially between microsites (Lambert et al. 2004). Additionally, annual variation in climate can change available emergent niche space. Our study represents emergence in a relatively average summer that was slightly wetter with normal temperatures (Environment Canada 2019). Since more emergence occurred on moist substrates, there may be more emergent niche space available in wetter years.

Emergent niches are often broader than post-emergent niches to allow widespread potential for establishment (Donohue et al. 2010). Conversely, a narrow emergent niche restricts spatial distribution of a species but promotes emergence under optimal conditions, reducing mortality for later life stages (Donohue et al. 2010). We identified a narrow emergent niche in an undisturbed region; however, exposed mineral soil following a fire is known to favour black spruce germination (Johnstone and Chapin 2006; Veilleux-Nolin and Payette 2012). Therefore, recently disturbed areas represent potential niche space that was not captured within our study but likely expands the size of the emergent niche. Then, over 5 - 10 years, species colonize the substrate and the organic layer builds up, narrowing available emergent niche space (Johnson and Fryer 1989; Hesketh et al. 2009; Brown and Johnstone 2012). Range expansion may then be facilitated by fires burning into the tundra, creating suitable niche space for emergence that did not exist in its undisturbed state if sufficient seed disperses beyond the range.

Progressing through the life cycle, we identified a directional and expanding niche shift during the transition from emergents to seedlings. Although seedlings can be found on a variety of surfaces, germination potential can differ between substrates (as reviewed in Zasada et al. 1992) and over time. Environmental conditions optimal for emergence can be detrimental for seedling survivorship (Schupp 1995; Cranston and Hermanutz 2013). We found seedlings to occupy microsites with a wider range of soil moisture conditions with a higher diversity of plant cover than where emergents occurred. Annual climate variation might expand the range of microsites on which germination can occur, resulting in seedlings occupying sites which were unsuitable for emergence during our study year.

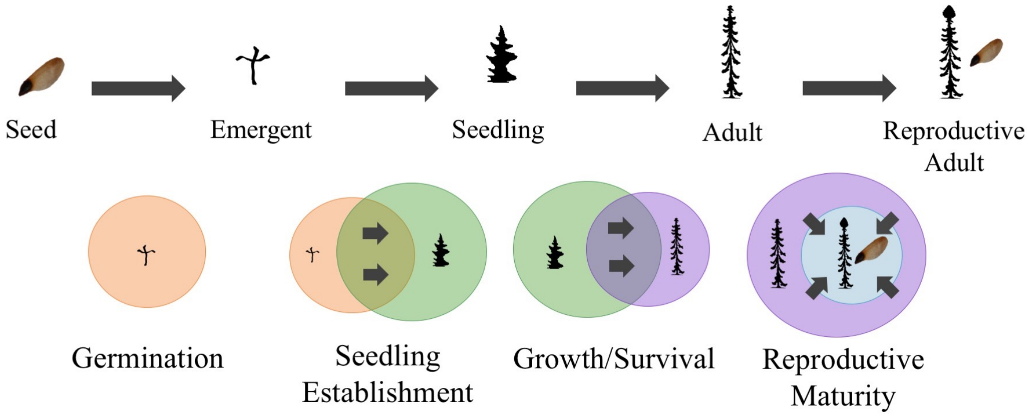
Seedlings had the broadest niche of the life stages we examined but were still limited to a subset of available substrates when compared to treeless tundra. In regards to plant cover, seedlings must deal with the balance between being protected from harsh elements by neighbouring plants and competing with these plants for resources (Smith et al. 2003; Batllori et al. 2009; Renard et al. 2016). We found that substrates with seedlings tended to have decreased tall shrub, lichen, and graminoid cover compared to treeless tundra substrates, but a higher cover of dwarf shrubs. Dwarf shrubs may be more suitable for seedling establishment than the other groups due to the high inhibitive density in which graminoids grow (Lett and Dorrepaal 2018), physiological and mechanical stressors trees experience when colonizing lichen mats (Houle and Filion 2003), and competitive ability of tall shrubs (Cranston and Hermanutz 2013; Truchon-Savard et al. 2019). Additionally, seedlings were present within a wider range of soil moisture conditions than emergents and exhibited no soil moisture preference relative to available treeless tundra substrates. Furthermore, seedlings exhibited no preference for warmer soils. Although warmer temperatures can improve germination and seedling growth, it does not appear to impact seedling survival (Lett and Dorrepaal 2018), at least within the range of temperature conditions we measured.

Between seedlings and non-reproductive adults, overall we observed a contracting and directional niche shift when all sites were ordinated together, indicating widespread seedling establishment in conditions that are unsuitable for adults. Our site-specific differences in niche shifts likely reflect the range of treeless tundra conditions available, where sites with a larger non-reproductive adult niche have more suitable niche space present for that group compared to other regions. Meanwhile, the ordination including all sites reflects the overall narrow niche space occupied by that life stage. The environment that a sheltered seedling experiences changes drastically when it emerges into the open air; this transition can act as a bottleneck due to wind stress and exposure to cooler air temperatures (Grace et al. 2002; Körner 2016). There were several unhealthy seedlings (e.g., brown needles, substantial needle loss) on the periphery of the seedling niche that may be experiencing the consequences of a niche contraction from occupying unsuitable conditions for the next demographic stage. Non-reproductive adults tended to occupy less competitive substrates with fewer tall shrubs and lichens than treeless tundra substrates. Conversely, they tended to occupy a higher cover of dwarf shrubs, which may have provided increased access to light, allowing adults to reach this stage.

Adults exhibited substantial overlapping niche space with seedlings and treeless tundra conditions but are also present in unique microsites. Conditions where adults overlap with earlier life stages likely indicate optimal conditions where seedlings are more likely to reach adulthood. Conversely, novel regions of niche space occupied exclusively by adults indicate areas where not only is the microsite changing as trees age, but it may be altered by the adults themselves (Holtmeier and Broll 2017). As trees use resources, create shade, and interact with their environment, they are altering their own microsite. At a certain point, we found that trees are able to create niche space unseen elsewhere in the tundra. For example, reproductive adults were associated with a higher moss cover, where trees may be creating shade and humidity that mosses such as *Sphagnum spp.* prefer (Campeau and Rochefort 1996). An adult's current microsite is likely different from the conditions it established within, where past conditions might have facilitated seedling establishment for current adults (Boby et al. 2010), particularly in fire-driven regeneration cycles that occur in the western boreal forest, as described above. Additionally, the way adults alter microsites may facilitate further establishment. Establishing close to adults is often considered beneficial for seedlings as they protect from harsh weather events (Batllori et al. 2009; Renard et al. 2016). Our findings suggest that the higher moss substrates created by adults may favour emergence within these protected environments. These novel adult niche space conditions that are not generally found in treeless tundra substrates provide a glimpse into how the tundra substrate may change if tree range expansion occurs.

Overall, we found a niche contraction from non-reproductive to reproductive adults when all sites were ordinated together, with site-specific niche shifts reflecting differences in available reproduction niche space. Northern conifer populations are often seed limited (Brown et al. 2019); our results suggest this may be related to strict microsite associations for seed production. Reproductive adults tended to occupy warmer, drier soils, with deeper organic layers with fewer shrubs and higher moss cover. The northern limit of black spruce in which our study is located is underlain with continuous permafrost (Tarnocai et al. 1993). Permafrost creates colder, wetter soils due to poor drainage (Ping et al. 2015), which leads to a slow nutrient release from organic matter and a low nutrient turnover (Hobbie et al. 2002). Reproductive adults are not just surviving in their microsite; they invest in seed production, an energetically costly process (Lee 1988). The warmer, drier soils that reproductive adults occupied may, in turn, have a higher nutrient turnover, increasing the nutrient availability for reproductive adults relative to their non-reproductive counterpart. Research has identified the role of nutrient availability on seedling establishment at treeline (Sullivan and Sveinbjörnsson 2010; Davis et al. 2018); our findings suggest its role in reproductive maturity warrants further investigation.

Black spruce shifts its niche and microsite preferences throughout its life cycle, as we have summarized in a conceptual diagram (Fig. 2.5). We found treeless tundra microsites to be heterogeneous across all sites. Variation at such a small scale creates select microrefugia suitable for establishment. For an individual to reach reproductive maturity, a microsite needs to temporally match with the appropriate demographic niches throughout a black spruce's life. Treeless tundra substrates had higher tall shrub and lichen cover than any area occupied by a tree of any life stage, indicating they restrict tree colonization. The negative association between the presence of tall shrubs and trees indicates that either tall shrubs inhibit black spruce establishment (Cranston and Hermanutz 2013; Truchon-Savard et al. 2019) or vice versa (Okano and Bret-Harte 2015). Since this association was found to begin during early establishment, our results indicate that the former scenario may be occurring where tall shrubs inhibit early black spruce establishment. Black spruce’s negative association with lichen may begin early, where lichen negatively impacts seedling establishment (Houle and Filion 2003). Higher lichen cover has been found to positively influence growth of later life stages, which would suggest a directional niche shift (Houle and Filion 2003). We may not see this positive effect if lichens do not increase in abundance in areas occupied by adults.



Microsite difference from previous life stage		↔ Diversity Plant Cover ↔ Soil Moisture	↓ Forb Cover ↑ Light Availability	↓ Medium Shrub Cover ↓ Soil Moisture ↓ Dwarf Shrub Cover*
Microsite difference from treeless tundra	↑ Moss Cover ↑ Soil Moisture	↓ Tall Shrub Cover ↓ Lichen Cover ↓ Graminoid Cover ↑ Dwarf Shrub Cover ↑ Light Availability	↓ Tall Shrub Cover ↑ Dwarf Shrub Cover ↑ Light Availability ↓ Lichen Cover*	↓ Tall Shrub Cover ↓ Medium Shrub Cover ↓ Lichen Cover ↑ Moss Cover ↑ Light Availability ↑ Soil Temperature ↓ Soil Moisture ↑ Organic Layer*

* Indicates significant at $P = 0.07$. Remaining microsite variables significant at $P = 0.05$.

Figure 2.5 Conceptual diagram of ontogenetic niche shifts throughout black spruce's life cycle. Circles represent demographic niches and associated ontogenetic niche shifts as described in Table 2.1. The white box lists microsite variables that were significantly different for the later life stage from the previous life stage. The grey box lists microsite variables that were significantly different between that life stage and treeless tundra substrates present within the region.

In addition to the microsite variables assessed here, other factors may also influence black spruce's demographic niches, including wind (Holtmeier and Broll 2010), snow cover (Renard et al. 2016), and biotic interactions (Speed et al. 2010; Crofts and Brown, *in review*). The transition from a seedling growing in a closed microsite to emerging into the open air increases their susceptibility to high winds (Wilson et al. 1987; Holtmeier and

Broll 2010). Sufficient snowpack can protect early life stages from extreme winter conditions, yet snow cover that is too thick shortens the growing season, impeding establishment (Lett and Dorrepaal 2018). Particular tree life stages may be more sensitive to herbivory (Quero et al. 2008) or mycorrhizal fungi associations (Hewitt et al. 2016), increasing their vulnerability to mortality.

In characterizing black spruce's demographic niches, we identified several microsite variables that can constrain or facilitate establishment throughout a species' life cycle. In future climate scenarios, the gradient of several of these microsite variables may shift, influencing tree establishment. We found all life stages to be negatively associated with tall shrubs, a group that has exhibited climate-induced increases in abundance and distributions in the Arctic (Myers-Smith et al. 2011). Substantial increases in tall shrub abundances may impede black spruce range expansion. Additionally, reproductive adults were associated with warmer soils, which may have increased nutrient turnover (Hobbie et al. 2002). Warmer soils under continued climate change may increase nutrient availability and potentially alleviate current seed availability bottlenecks (Brown et al. 2019) due to increased cone production.

2.6 Conclusion

Understanding a species' demographic niches provides insights into which life stage constrains range expansion. Whether or not climate change is creating suitable niche space for conifers such as black spruce in tundra ecosystems remains unclear. Northward tree range expansion is often limited by viable seed availability (e.g., Brown et al. 2019). We found that this likely arises from reproductive adults having narrow niche requirements, potentially forming non-reproductive sink populations in areas were reproduction niche space is absent. Only considering adult occurrence when forecasting range shifts will not capture the complexity of the species' demographic niches and may misrepresent the species response to climate change (Pironon et al. 2018). Additionally, we show that seedlings have the broadest demographic niche of all life stages. Therefore, the presence of seedlings beyond a species' range will only result in a range expansion if conditions are also suitable for adults. The standard reference for treeline advance estimates that 52% of treelines are advancing (Harsch et al. 2009). Yet, 47% of these advancing treelines associate the presence of individuals <2 m tall beyond the range as evidence of recent treeline advance. If some of these studies include early life stages with broader demographic niches than adults and adult niche space is absent, the proportion of treelines advancing could be as low as 24.4%. Although the number is likely not this low, 24.4% - 52% is a wide range of uncertainty and understanding demographic niches can help fine tune that range to provide a better understanding of where and under what circumstances species' distributions will shift under continued climate change.

2.7 References

Anderson, J. T., A. A. Landi, and P. L. Marks. 2009. Limited flooding tolerance of juveniles restricts the distribution of adults in an understory shrub *(Itea virginica; Iteaceae).* American Journal of Botany 96:1603–1611.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Batllori, E., J. J. Camarero, J. M. Ninot, and E. Gutiérrez. 2009. Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* tree line ecotones. Implications and potential responses to climate warming. Global Ecology and Biogeography 18:460–472.

Bertrand, R., J.-C. Gégout, and J. Bontemps. 2011. Niches of temperate tree species converge towards nutrient-richer conditions over ontogeny. Oikos 120:1479–1488.

Black, R. A., and L. C. Bliss. 1980. Reproductive ecology of *Picea mariana* (Mill.) BSP., at tree line near Inuvik, Northwest Territories, Canada. Ecological Monographs 50:331–354.

Boby, L. A., E. A. G. Schuur, M. C. Mack, D. Verbyla, and J. F. Johnstone. 2010. Quantifying fire severity, carbon, and nitrogen emissions in Alaska’s boreal forest. Ecological Applications 20:1633–1647.

Brown, C. D., G. Dufour-Tremblay, R. G. Jameson, S. D. Mamet, A. J. Trant, X. J.

Walker, S. Boudreau, et al. 2019. Reproduction as a bottleneck to treeline advance across the circumarctic forest tundra ecotone. Ecography 43:137–147.

Brown, C. D., and J. F. Johnstone. 2012. Once burned, twice shy: Repeat fires reduce seed availability and alter substrate constraints on *Picea mariana* regeneration. Forest Ecology and Management 266:34–41.

Brown, C. D., J. Liu, G. Yan, and J. F. Johnstone. 2015. Disentangling legacy effects from environmental filters of postfire assembly of boreal tree assemblages. Ecology 96:3023–3032.

Campeau, S., and L. Rochefort. 1996. *Sphagnum* regeneration on bare peat surfaces: Field and greenhouse experiments. Journal of Applied Ecology 33:599–608.

Chapin, F. S., M. Sturm, M. C. Serreze, J. P. McFadden, J. R. Key, A. H. Lloyd, A. D. McGuire, et al. 2005. Role of land-surface changes in arctic summer warming. Science 310:657–660.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117–143.

Cranston, B. H., and L. Hermanutz. 2013. Seed-seedling conflict in conifers as a result of plant-plant interactions at the forest-tundra ecotone. Plant Ecology and Diversity 6:319–327.

Davis, E. L., H. A. Hager, and Z. Gedalof. 2018. Soil properties as constraints to seedling regeneration beyond alpine treelines in the Canadian Rocky Mountains. Arctic, Antarctic, and Alpine Research 50:1–15.

Donohue, K., R. Rubio de Casas, L. Burghardt, K. Kovach, and C. G. Willis. 2010. Germination, postgermination adaptation, and species ecological ranges. Annual Review of Ecology, Evolution, and Systematics 41:293–319.

Environment Canada. 2019. Canadian climate normals 1981-2010 Station Data: Old Crow A.

Eriksson, O. 2002. Ontogenetic niche shifts and their implications for recruitment in three clonal Vaccinium shrubs: *Vaccinium myrtillus, Vaccinium vitis-idaea,* and *Vaccinium oxycoccos.* Canadian Journal of Botany 80:635–641.

Ettinger, A. K., and J. HilleRisLambers. 2013. Climate isn't everything: Competitive interactions and variation by life stage will also affect range shifts in a warming world. American Journal of Botany 100:1344–1355.

Fraser, J. W. 1976. Viability of Black Spruce Seed in or on a Boreal Forest Seedbed. The Forestry Chronicle 52:229–231.

Gabler, C. A., and E. Siemann. 2013. Rapid ontogenetic niche expansions in invasive Chinese tallow tree permit establishment in unfavourable but variable environments and can be exploited to streamline restoration. Journal of Applied Ecology 50:748–756.

Government of Yukon 2017. Wildland Fire Management Data, Maps and Bulletins Archive.

Grace, J., F. Beringer, and L. Nagy. 2002. Impacts of climate change on the tree line. Annals of Botany 90:537–544.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: The importance of the regeneration niche. Biological Reviews 52:107–145.

Hargreaves, A. L., K. E. Samis, and C. G. Eckert. 2014. Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. The American Naturalist 183:157–173.

Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology Letters 12:1040–1049.

Hättenschwiler, S., and C. Körner. 1995. Responses to recent climate warming of *Pinus sylvestris* and *Pinus cembra* within their montane transition zone in the Swiss Alps. Journal of Vegetation Science 6:357–368.

Hesketh, M., D. F. Greene, and E. Pounden. 2009. Early establishment of conifer recruits in the northern Rocky Mountains as a function of postfire duff depth. Canadian Journal of Forest Research 39:2059–2064.

Hewitt, R. E., T. N. Hollingsworth, F. Stuart Chapin, and D. Lee Taylor. 2016. Fire-severity effects on plant-fungal interactions after a novel tundra wildfire disturbance: Implications for arctic shrub and tree migration. BMC Ecology 16:1–11.

Hobbie, S. E., K. J. Nadelhoffer, and P. Högberg. 2002. A synthesis: The role of nutrients as constraints on carbon balances in boreal and arctic regions. Plant and Soil 242:163–170.

Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. Proceedings of the National Academy of Sciences 106:19659–19665.

Holtmeier, F. K., and G. Broll. 2010. Wind as an ecological agent at treelines in North America, the Alps, and the European subarctic. Physical Geography 31:203–233.

Holtmeier, F. K., and G. Broll. 2017. Feedback effects of clonal groups and tree clusters on site conditions at the treeline: Implications for treeline dynamics. Climate Research 73:85–96.

Hou, C., W. Zuo, M. E. Moses, W. H. Woodruff, J. H. Brown, and G. B. West. 2008. Energy uptake and allocation during ontogeny. Science 322:736–739.

Houle, G., and L. Filion. 2003. The effects of lichens on white spruce seedling establishment and juvenile growth in a spruce-lichen woodland of subarctic Québec. Écoscience 10:80–84.

Hu, F. S., L. B. Brubaker, D. G. Gavin, P. E. Higuera, J. A. Lynch, T. S. Rupp, and W. Tinner. 2006. How climate and vegetation influence the fire regime of the alaska boreal biome: The holocene perspective. Mitigation and Adaptation Strategies for Global Change 11:829–846.

Hutchinson, G. E. 1957. Concluding Remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427.

Johannessen, O. M., S. I. Kuzmina, L. P. Bobylev, and M. Myles. 2016. Surface air temperature variability and trends in the Arctic: New amplification assessment and regionalisation. Tellus A: Dynamic Meteorology and Oceanography 68:1–12.

Johnson, E. A., and G. I. Fryer. 1989. Population dynamics in lodgepole pine-engelmann spruce forests. Ecology 70:1335–1345.

Johnston, W., and T. Smith. 1985. Black Spruce. Pages 96–98 *in* Silvicultural systems for the major forest types of the United States.

Johnstone, J. F., and F. S. Chapin. 2006. Effects of soil burn severity on post-fire tree recruitment in boreal forest. Ecosystems 9:14–31.

Kasischke, E. S., D. L. Verbyla, T. S. Rupp, A. D. McGuire, K. A. Murphy, R. Jandt, J. L. Barnes, et al. 2010. Alaska's changing fire regime — implications for the vulnerability of its boreal forests. Canadian Journal of Forest Research 40:1313–1324.

Körner, C. 2016. When it gets cold, plant size matters - A comment on treeline. Journal of Vegetation Science 27:6–7.

Lee-Yaw, J. A., H. M. Kharouba, M. Bontrager, C. Mahony, A. M. Csergo, A. M. E. Noreen, Q. Li, et al. 2016. A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. Ecology Letters 19:710–722.

Lee, T. D. 1988. Patterns of fruit and seed production. Pages 179–202 inPlant reproductive ecology. Oxford University Press, New York, U.S.A.

Legendre, P., and L. F. Legendre. 2012. Numerical Ecology (3rd ed.). Elsevier, Oxford, U.K.

Lett, S., and E. Dorrepaal. 2018. Global drivers of tree seedling establishment at alpine treelines in a changing climate. Functional Ecology 32:1666–1680.

Lucas-Borja, M. E., T. Fonseca, J. C. Linares, F. A. García Morote, and F. R. López Serrano. 2012. Does the recruitment pattern of Spanish black pine *(Pinus nigra Arn ssp. salzmannii)* change the regeneration niche over the early life cycle of individuals? Forest Ecology and Management 284:93–99.

Maguire, B. 1973. Niche response structure and the analytical potentials of its relationship to the habitat. The American Naturalist 107:213–246.

Malcolm, J. R., A. Markhan, R. P. Neilson, and M. Garaci. 2002. Estimated migration rates under scenarios of global climate change. Journal of Biogeography 29:835–849.

Máliš, F., M. Kopecký, P. Petřík, J. Vladovič, J. Merganič, and T. Vida. 2016. Life stage, not climate change, explains observed tree range shifts. Global Change Biology 22:1904–1914.

Manley, B. 2006. Randomization, bootstrap and Monte Carlo methods in biology (3rd ed.). Chapman and Hall/CRC.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MJM Software Design, Glenden Beach, Oregon U.S.A.

Miriti, M. N. 2006. Ontogenetic shift from facilitation to competition in a desert shrub. Journal of Ecology 94:973–979.

Müller, L. L. B., D. C. Albach, and G. Zotz. 2018. Growth responses to elevated temperatures and the importance of ontogenetic niche shifts in Bromeliaceae. New Phytologist 217:127–139.

Okano, K., and M. S. Bret-Harte. 2015. Warming and neighbor removal affect white spruce seedling growth differently above and below treeline. SpringerPlus 4:1–14.

Oksanen, J., F. Guillaume-Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, et al. 2013. “Vegan” community ecology package.

Olsen, M. H. 1996. Ontogenetic niche shifts in largemouth bass: Variability and consequences for first-year growth. Ecology 77:179–190.

Parrish, J. A. D., and F. A. Bazzaz. 1985. Ontogenetic niche shifts in old-field annuals. Ecology 66:1296–1302.

Pérez-Ramos, O., I. R. Urbieta, M. A. Zavala, and T. Marañon. 2012. Ontogenetic conflicts and rank reversals in two Mediterranean oak species: Implications for coexistence. Journal of Ecology 100:467–477.

Peterson, A. T., J. Soberon, R. G. Pearson, R. P. Anderson, E. Martinez-Meyer, M. Nakamura, and M. Bastos Araujo. 2011. Ecological niches and geographic distributions. Princeton University Press, Princton, New Jersey.

Ping, C. L., J. D. Jastrow, M. T. Jorgenson, G. J. Michaelson, and Y. L. Shur. 2015. Permafrost soils and carbon cycling. Soil 1:147–171.

Pironon, S., J. Villellas, W. Thuiller, V. M. Eckhart, M. A. Geber, D. A. Moeller, and M. B. García. 2018. The "Hutchinsonian niche" as an assemblage of demographic niches: Implications for species geographic ranges. Ecography 41:1103–1113.

Pulliam, H. R. 2000. On the relationship between niche and distribution. Ecology Letters 3:349–361.

Quero, J. L., L. Gómez-Aparico, R. Zamora, and F. T. Maestre. 2008. Shifts in the regeneration niche of an endangered tree *(Acer opalus ssp. granatense)* during ontogeny: Using an ecological concept for application. Basic and Applied Ecology

9:635–644.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Renard, S. M., E. J. B. McIntire, and A. Fajardo. 2016. Winter conditions - not summer temperature - influence establishment of seedlings at white spruce alpine treeline in Eastern Quebec. Journal of Vegetation Science 27:29–39.

Robertson, G. P., P. Sollins, B. G. Ellis, and K. Lajtha. 1999. Exchangeable ions, pH, and cation exchange capacity. Pages 106–114 *in* Standard soil methods for long-term ecological research. Oxford University Press, New York, U.S.A.

Schupp, E. W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany 82:399–409.

Schurr, F. M., J. Pagel, J. S. Cabral, J. Groeneveld, O. Bykova, R. B. O'Hara, F. Hartig, et al. 2012. How to understand species' niches and range dynamics: A demographic research agenda for biogeography. Journal of Biogeography 39:2146–2162.

Smith, A. B., W. Godsoe, F. Rodríguez-Sánchez, H. Wang, and D. Warren. 2019. Niche estimation above and below the species level. Trends in Ecology & Evolution 34:260–273.

Smith, W. K., M. J. Germino, T. E. Hancock, and D. M. Johnson. 2003. Another perspective on altitudinal limits of alpine timberlines. Tree Physiology 23:1101–1112.

Speed, J. D. M., G. Austrheim, A. J. Hester, and A. Mysterud. 2010. Experimental evidence for herbivore limitation of the treeline. Ecology 91:3414–3420.

Streicker, J. 2016. Yukon climate change indicators and key findings 2015. Northern Climate ExChange, Yukon Research Centre, Yukon College.

Sullivan, P. F., and B. Sveinbjörnsson. 2010. Microtopographic control of treeline advance in Noatak National Preserve, Northwest Alaska. Ecosystems 13:275–285.

Sveinbjörnsson, B., H. Kauhanen, and O. Nordell. 1996. Treeline ecology of mountain birch in the Torneträsk area. Ecological Bulletins 45:65–70.

Tarnocai, C., C. A. S. Smith, and C. A. Fox. 1993. International tour of permafrost affected soils: The Yukon and Northwest Territories of Canada. Ottawa.

Truchon-Savard, A., M. Jean, and S. Payette. 2019. Black spruce *(Picea mariana)* colonization of subarctic snowpatches in response to warmer climate. Journal of Ecology 107:1154–1166.

Veilleux-Nolin, M., and S. Payette. 2012. Influence of recent fire season and severity on black spruce regeneration in spruce – moss forests of Quebec, Canada. Canadian Journal of Forest Research 42:1316–1327.

Wheeler, J. A., L. Hermanutz, and P. M. Marino. 2011. Feathermoss seedbeds facilitate black spruce seedling recruitment in the forest-tundra ecotone (Labrador, Canada). Oikos 120:1263–1271.

Wilson, C., J. Grace, S. Allen, and F. Slack. 1987. Temperature and stature: A study of temperatures in montane vegetation. Functional Ecology 1:405–413.

Zasada, J. C., T. L. Sharik, and M. Nygren. 1992. The reproductive process in boreal forests. Pages 95–135 *in* A systems analysis of the global boreal forest. Cambridge University Press, Cambridge, U.K.

Chapter 3: Pre-seedling life stages impede northern black spruce range expansion: A demographic niche-based assessment of microsite availability

3.1 Abstract

In order for range expansion to occur, suitable microsites for establishment must be available beyond a given species' range. Species can have life-stage specific requirements with unique niche breadths, forming multiple demographic niches. If niche space is limited beyond the range for a certain life stage, that stage will be a rate-limiting step for range expansion. Using a novel demographic niche-based approach, we characterized changes in suitable microsite availability towards the range limit for black spruce (*Picea mariana*) establishment in subarctic Yukon throughout its life cycle. We also quantified changes in viable seed availability and germination rates towards the range limit. Combined, these methods determine which life stages are the main limiting demographic bottlenecks on northern black spruce range expansion. Using non-metric multidimensional scaling, we compared microsites that individuals of different life stages occupied to unoccupied tundra substrates to assess the availability of suitable microsites along a spatial gradient heading towards the range edge. Microsite availability for seedlings and adults did not change across our treeline gradient. Meanwhile, we found the low availability of both viable seed and suitable germination microsites were the main limiting demographic hurdles on northern black spruce range expansion. This novel approach can further inform the role that demographics and microsite availability play on species' distributions in a changing climate.

3.2 Introduction

Species' distributions are not uniformly tracking their climatic niche under continued climate change (e.g., Harsch et al. 2009; Freeman et al. 2018). Along with climate, the rate of a population's range shift depends on the species' life history and other non-climatic factors (Sexton et al. 2009; Schurr et al. 2012; Brown and Vellend 2014). At the landscape scale, multiple abiotic and biotic factors influence plant distributions including topography (Resler et al. 2005), competition (Wang et al. 2016), and moisture (Moyes et al. 2015). From an individual's perspective, however, establishment depends on the abiotic and biotic composition of their immediate microsite. At this fine scale, landscapes are heterogeneous, containing a variety of microsites that may or may not be suitable for regeneration. Suitable microsite availability is a critical hurdle that must be overcome for establishment (Harper 1977), particularly at the range limit where suitable microsites may be scarce (e.g., Batllori et al. 2009*b*; Dufour-Tremblay et al. 2012).

The ecological composition of microsites can influence a species in different ways throughout its life cycle, from a seed dispersing to that same propagule reaching reproductive maturity (Chapter Two; Quero et al. 2008; Donohue et al. 2010; Cranston and Hermanutz 2013). Thus, a species' life stages can have unique niche dimensions, responding differently to abiotic and biotic variables and resulting in multiple demographic niches (Chapter Two; Quero et al. 2008; Pironon et al. 2018). Changes in requirements between life stages, termed ontogenetic niche shifts, create a series of demographic bottlenecks (Table 3.1) that sequentially filter out potential candidates for establishment. The ability for a sufficient number of individuals to establish and reach reproductive maturity beyond a species' range depends on the relative intensities of the demographic bottlenecks that the potentially expanding population experiences. In particular, high mortality during early life stages make those respective demographic niches important in shaping the spatial distribution of a species at the range limit (Harper 1977; Eriksson and Ehrlén 1992; Brodersen et al. 2019). Conversely, the relative importance of microsite composition for adult life stages and reproduction remain unclear, and studies often focus on larger scale factors for these groups (e.g., Grace et al. 2002; Krebs et al. 2012; Brown et al. 2019).

Identifying the most limiting life stages and their associated demographic niches will reveal the circumstances under which a region is primed for range expansion. Microsite conditions must temporally align with these demographic niches. If suitable niche space is restricted for certain life stages, they will become a rate-limiting step for climate-induced range expansion. To more accurately predict range expansion, the challenge, then, is to reconcile a species' demographic niche breadths with characteristics of available microsites at and beyond a species' range edge. This multivariate approach will elucidate the role suitable microsite availability plays in range shifts throughout a species' life cycle under continued climate warming.

The most acute contemporary climate warming is occurring in northern latitudes and alpine regions (Chapin et al. 2005; Pepin et al. 2015). These rapidly changing regions are where the upper range limit of many boreal tree species occur, forming the forest-tundra ecotone (henceforth treeline). The intense warming these trees experience make treelines an excellent model system to assess the importance of suitable microsite availability in climate-induced range shifts. The treeline is composed of tundra substrates with gradually decreasing tree density until the respective tree species' range limits are reached. Despite acute warming, climate induced treeline advance has been both inconsistent and complex, involving a suite of non-climatic factors acting at different spatial and temporal scales (Holtmeier and Broll 2005; Harsch et al. 2009; Camarero et al. 2017).

As with any plant range expansion, treeline advance requires suitable microsites for seed germination, seedling establishment, adult growth, and viable seed production (Table 3.1). The frequency and ecological composition of suitable microsites are not clearly defined at the treeline (Brodersen et al. 2019). At treeline and other range edge populations, the assessment of microsite suitability often focuses on one or two life stages (e.g., Cranston and Hermanutz 2013; Davis and Gedalof 2018) and one or two variables (e.g., distance to protective elements (Germino et al. 2002; Batllori et al. 2009*b*), microtopography (Sullivan and Sveinbjörnsson 2010), or plant community composition (Wheeler et al. 2011; Dufour-Tremblay et al. 2012) but see Kambo and Danby 2018). This univariate approach is valuable for experimentally teasing apart individual influencing factors but does not allow for a comprehensive understanding of microsite availability within a variable landscape that is more complex than we have the technological capacity to model.

Table 3.1 Examples of life stage specific constraints observed in range edge treeline populations.

Life stage	Constraints	Evidence
 **1. Viable seed disperses beyond range**	Seed availability is often low at treeline, due to low seed quantity via low stand density, low seed viability from harsh climates and reduced genetic diversity, and post-dispersal seed predation	Caron and Powell 1989; O'Connell et al. 2006; Kroiss and HilleRisLambers 2015; Kambo and Danby 2017
 **2. Germination**	Seed must land on suitable microsites for germination, which can be rare at the range limit	Wheeler et al. 2011; Dufour-Tremblay et al. 2012; Walker et al. 2012
 **3. Seedling establishment**	Mortality is often high for seedlings at treeline as they are more susceptible to harsh conditions and may germinate on poor substrates for establishment	Cuevas 2000; Germino et al. 2002; Castanho et al. 2012; Cranston and Hermanutz 2013
 **4. Adult growth/survival**	Rising from the sheltered understory to colder open air temperatures with higher winds can be detrimental to adult establishment	Wilson et al. 1987; Grace et al. 2002; Körner 2016
 **5. Reproductive maturity**	Existing populations may be maintained through clonal growth, but sexual reproduction is required for range expansion and is often limited at treeline via both biotic and abiotic factors	Sirois 2000; Malcolm et al. 2002; Krebs et al. 2012; Jameson et al. 2015; Brown et al. 2019

Here, we present a novel multivariate approach to identify microsite availability by comparing black spruce's (*Picea mariana*) demographic niches to changes in available tundra substrates along a treeline ecotone gradient at the range edge. We also quantified viable seed production, seed dispersal, and conducted a field-based seeding experiment to determine seed availability and germination limitations towards the range edge. Together, these objectives inform which life stage(s) are the most limiting bottlenecks on northern black spruce range expansion in the Yukon (as outlined in Table 3.1). We assessed microsite suitability at the treeline for four life stages of black spruce: emergents (recently germinated and are <1-year-old), seedlings (≤60 cm tall), non-reproductive adults (>60 cm tall without cones), and reproductive adults (>60 cm tall with cones). Treeline populations often exhibit stunted growth forms (krummholz) that can be reproductively mature despite their small stature (e.g., Trant et al. 2011); therefore, we classified any individual >60 cm as an adult. Based on previous findings (e.g., Batllori et al. 2009*b*; Dufour-Tremblay et al. 2012; Kroiss and HilleRisLambers 2015), we predicted that microsite suitability would decrease towards the range edge for all life stages, but that early stages (seed availability, emergence, seedling establishment) would be most limiting. Using a demographic niche-based approach, our multivariate assessment of microsite suitability throughout the entire life span allows for a more comprehensive understanding of life-stage specific microsite constraints across the range edge.

3.3 Methods

3.3.1 Study area and species description

We conducted our research at three black spruce dominated treeline sites near Eagle Plains, Yukon (66° 22' 12" N, 136° 43' 48" W). Mean temperatures from 1981-2010 ranged from 14.6°C in July to -29.2°C in January with an annual mean precipitation of 278.6 mm (Environment Canada 2019). The area consists of rolling hills with gradually decreasing tree density and fine-grained loess soils over bedrock (Smith et al. 2004). All sites are underlain with continuous permafrost that have a seasonal thaw depth of less than 1 m (Tarnocai et al. 1993). Each site represented a range edge black spruce population where tree density gradually decreased heading towards the range limit and all life stages were present. Site One had an understory shrub community primarily consisting of *Betula spp., Salix spp., Rhododendron spp., Vaccinium uliginosum, Empetrum nigrum,* and *Vaccinium visis-idaea*, with a high lichen cover (primarily *Cladonia spp*.) and was interlaid with frost boils from freeze-thaw permafrost cycles. Sites Two and Three were moss dominated, primarily with *Sphagnum spp.* and feathermoss species (e.g., *Hylocomium* spp.), and had a similar shrub community to Site One (see Chapter Two for further description of study sites and a map of the study region).

Black spruce is a long-lived coniferous species commonly found on wet organic soils across North American boreal forests (Johnston and Smith 1985). Subarctic populations begin producing cones when 25-30 years old, and reliably produce cones at 85 years (Black and Bliss 1980). Black spruce is a semi-serotinous species and maintains an aerial seedbank containing several cone cohorts that will gradually release seed in the absence of fire and massively disperse after a fire (Zasada et al. 1992). Our classification of reproductive adults included trees that had successfully produced cones from previous years. Seeds are dispersed by wind and travel up to 80 m from the windward edge of a mature stand (Johnston and Smith 1985). Once dispersed, seed loses its viability within 10 to 16 months (Fraser 1976). Black spruce can also reproduce by layering: forming adventitious roots on lateral branches to produce clonal stems (Holtmeier 2009).

3.3.2 Study design

Within each of the three sites, four 100 m x 10 m belt transects were established perpendicular to the treeline, heading towards the range edge (i.e., same transects as Chapter Two). The transects were placed ~20 m apart with the zero marker for each transect indicating the last reproductive adult along the center of the transect. From this point, the transect extended 45 m towards the tundra and 55 m towards the forest (see Supplementary Fig. 2.1 for diagram of study design). All analyses assess how different demographic patterns and substrate limitations change along these transects (i.e., towards the range edge of the black spruce population), therefore all analyses describe this gradient as distance towards range edge from 0 to 100 m.

3.3.3 Viable seed availability

To assess whether seed dispersal impedes range expansion, we used seed traps to quantify naturally dispersed seed. Seed traps were installed in 10 m increments along the four transects at each site for a total of 120 seed traps. A seed trap consisted of a plastic garden tray (50 cm x 25 cm x 5.7 cm) with artificial grass attached to the bottom to prevent wind scouring (following Johnstone et al. 2009). Seed traps were initially deployed at Site One in July 2017 with seed collected in Aug 2018 for a year-round assessment of seed dispersal. Seed traps were installed at the remaining sites in June 2018 and collected in August 2018 to assess summer seed dispersal. Material from seed traps were collected in plastic bags and brought to the Northern EDGE Lab at Memorial University, St. John's, NL to be stored at ~0°C until the contents were hand sorted to count black spruce seed.

To investigate if viable seed production limits range expansion, we quantified cone production, seed production, and seed viability at each site. We estimated the number of cones present on each adult tree along the transects. We then randomly selected up to 32 trees at each site to harvest cones to estimate site level seed viability. Cone harvest trees were selected away from transects, beyond dispersal distance, to ensure cone harvesting did not interfere with seed rain data collection. We randomly harvested 20 cones from each tree. Since black spruce retains several annual cone cohorts, where possible, we exclusively selected closed brown, i.e., approximately second year, cones to ensure we harvested cones that were both mature and had not already released seed (Eremko et al. 1989). If we were unable to collect sufficient closed brown cones, we collected older gray cones. If a tree had fewer than 20 cones, we collected all of its cones. We placed cones in paper bags and shipped them to the Northern EDGE Lab for seed extraction and germination trials.

In the laboratory, seeds were extracted following established protocols (modified from Safford 1974; Leadem et al. 1997; Viglas et al. 2013). Cones were grouped by tree and soaked in deionized water for approximately 24 hours, dried at room temperature for 24-72 hours, and then heated in an oven at 60°C for 16 hours. Following this, cones were agitated in a sieve shaker for 10 minutes to release the seeds. The seed extraction cycle was repeated three times to ensure all seeds that could potentially disperse were extracted. After counting the total number of seeds released per tree, we immersed seeds in a 95% ethanol bath to quantify the number of filled seeds. Black spruce seeds that sink in ethanol have been found to contain both an embryo and megagametophyte while seeds that float are unfilled (Jameson et al. 2015).

Up to 100 seeds that contained embryos from each tree were randomly selected for a 28-day laboratory germination trial. Up to 50 seeds were placed on a 9 cm petri dish on filter paper kept moist with deionized water. Seeds experienced room temperature (~20°C) and 16 hours of light per day (6400 K full-spectrum, T5 lamp with omni-max reflector; Jump start, Hydrofarm, Petaluma, CA, USA). Seeds were considered germinated if the length of their radicle was at least four times that of the seed coat (Leadem et al. 1997). We estimated site level production of viable seed using the number of seeds/cone, the proportion of seeds with embryos, and the proportion of all seeds that germinated for each tree.

3.3.4 Characterizing microsite suitability

We conducted a seed addition experiment along the treeline gradient to identify germination limitations (see Chapter Two for full description of seed addition experiment). To assess tundra suitability for black spruce establishment and how it may change towards the range edge, we conducted a multivariate comparison between random treeless tundra microsites and black spruce’s demographic niches. To capture how potential microsites for colonization may change towards the range edge, we compared how microsite associations (as described in Chapter Two) changed towards the range edge for emergent, seedlings, non-reproductive adults, and reproductive adults. The microsite each life stage inhabits was defined as: the seed plot for the emergent niche, the area within 25 cm of tree base for remaining life stages, and a 50 cm x 50 cm quadrat for treeless tundra substrates. We recorded the following variables at each marked microsite: active layer depth, organic layer depth, soil moisture, soil temperature, soil pH, light availability, microtopography, and plant community composition. Plant community composition was divided into the following functional groups: moss, lichen, forbs, graminoids, and shrubs. Shrubs were recorded to the species level and then grouped into three categories based on the functional height of the species: tall shrubs (e.g., *Betula glandulosa, Salix glauca),* medium shrubs (e.g., *Rhododendron spp., Vaccinium uliginosum)*, and dwarf shrubs (e.g., *Empetrum nigrum, Vaccinium visis-idaea).* See Chapter Two for a comprehensive description of microsite variable data collection.

3.3.5 Data analysis

To assess how seed dispersal and emergence in the seed addition experiment changed along the transect, we used generalized linear mixed models (GLMMs) from the "lme4" package version 1.1-21 (Bates et al. 2015) in the R environment (R Core Team 2019). Number of dispersed seeds in a seed trap or emergents in a seed plot were the response variables for each model, with distance along transect as an explanatory variable and transect nested within site as random effects. Both data sets exhibited a large number of zero observations. We used zero-altered hurdle models to account for excess zeroes (Zuur et al. 2009). First, the data were modelled as a presence/absence of seed in a seed trap or emergents in a seed plot with a binomial distribution. The abundance of seed or emergents were then modelled with a truncated Poisson model (Zuur et al. 2009). For the seed dispersal models, we looked at summer dispersal (June - Aug 2018) across all three study sites and year-round dispersal (July 2017 - Aug 2018) at the site with year-round data (Site One). The year-round model was not zero-inflated, so we used a GLMM with a Poisson distribution. We removed an outlier from the emergence model that had extremely high germination (n = 36). None of the Poisson GLMMs were over-dispersed (Zuur et al. 2009).

We constructed a GLMM to determine if the estimated number of cones present within each 10 m x 10 m increment changed towards the range edge. We used the Gaussian distribution for the GLMM with cone count as the response variable and distance along the transect as the explanatory variable with transect nested within site as random effects. Due to model assumption violations, we then confirmed the statistical decision at the 0.05 level using a randomization test as follows (Manley 2006). F-values from 5000 GLMMs modelled with samples of the response variable were calculated to obtain an assumption-free empirical distribution. The probability of the F-value obtained from the original GLMM was then determined using this empirical distribution.

We used non-metric multidimensional scaling (NMDS) for a multivariate comparison between the characteristics of black spruce's demographic niches (i.e., microsites) that we quantified and available treeless tundra substrates. To assess changes in suitable microsite availability along the transect, we extracted individuals' NMDS scores from ordinations in Chapter Two for each of the three sites and all sites combined and plotted them against distance along the transect (i.e., distance towards the range edge). In NMDS, no particular axis explains more variation than other axes (McCune and Grace 2002). Therefore, changes in any NMDS axis along the transect were considered equally. We then used a loess smooth curve using the geom_smooth function in the ggplot2 R package version 3.1.1 (Wickham et al. 2016) to visually assess how NMDS scores changed for treeless tundra substrates and each demographic niche. We constructed 95% confidence intervals for NMDS scores for each life stage and treeless tundra substrates along the transect. Any non-overlapping confidence intervals between a life stage and treeless tundra substrates were considered to indicate a mismatch in substrate suitability.

We ran a suite of GLMMs with a Gaussian distribution for each microsite variable to determine whether treeless tundra substrates changed along our treeline gradient. These models confirmed the potential for changing microsite availability along our study gradient. For each GLMM, the respective microsite variable was the response, distance along the transect was the explanatory variable, and transect nested within site were random effects. If the GLMM violated model assumptions, the statistical decision at the 0.05 level was confirmed with a randomization test, as described above.

3.4 Results

3.4.1 Bottleneck 1: Viable seed availability

Seed rain was low at all study sites and decreased towards the range edge (Table 3.2). During summer dispersal (June - Aug 2018) across all sites, 37/120 (30.8%) seed traps captured dispersed seed, containing a total of 68 dispersed seeds. Meanwhile, the site with year-round dispersal data (July 2017 - Aug 2018) had dispersed seeds in 33/40 (82.5%) seed traps, containing a total of 114 seeds. In our zero-inflated hurdle model assessing summer dispersal at all sites, the odds of seed being present in a seed trap did not change towards the range limit (Table 3.2). However, seed abundance in seed traps significantly decreased towards the range limit during the summer 2018 dispersal period (Table 3.2). Similarly, the site with year-round dispersal data had significantly less seed rain towards the range limit (Table 3.2).

Despite decreased seed dispersal, we found cone production did not change towards the range edge (Table 3.2). Because collecting cones along the transect would interfere with seed trap data collection, we were unable to assess whether the discrepancy between seed rain and cone production was caused by declines in seeds produced per cone along the transect. Viable seed was produced at all sites and site level estimations of number of seeds per cone ranged from 29.6 to 40.3 (Table 3.3; Fig. 3.1). We estimated that 39% - 43.7% of those seeds contained embryos (Table 3.3; Fig. 3.1). Seed viability at the sites varied from 24.2% - 36.6% (Table 3.3; Fig. 3.1).

Table 3.2 Summary of GLMMs assessing changes in seed dispersal and germination with distance towards the range edge (i.e., negative values indicate the response declines towards the range edge). Transect nested within site were included as random effects (values not shown). P values significant at the 0.05 level are bolded. * indicates a revised p-value from a randomization test due to model assumption violations.

Model	Model Term	Estimate	SE	z-value	p-value
Odds summer seed dispersal (binomial)	Intercept	**-0.976**	**0.466**	**-2.095**	**0.036**
	Distance	-0.012	0.007	-1.617	0.106
Abundance summer seed dispersal (truncated poisson)	Intercept	**0.451**	**0.149**	**3.028**	**0.002**
	Distance	**-0.010**	**0.005**	**-2.282**	**0.024**
Year-round seed dispersal Site One only (poisson)	Intercept	**0.761**	**0.368**	**2.065**	**0.039**
	Distance	**-0.011**	**0.003**	**-3.189**	**0.001**
Odds germination (binomial)	Intercept	**-1.333**	**0.437**	**-3.048**	**0.002**
	Distance	0.004	0.009	0.411	0.681
	Treatment	**-3.124**	**1.040**	**-3.003**	**0.003**
Abundance germination (truncated poisson)	Intercept	**1.353**	**0.346**	**3.914**	**0.0001**
	Distance	**-0.012**	**0.004**	**-3.121**	**0.002**
Cone estimate (gaussian)	Intercept	371.428	281.247	1.321	0.316
	Distance	-9.729	5.260	-1.850	0.193*

Table 3.3 Number of reproductive adults present per hectare, number of cones per tree (mean ± standard deviation), number of seeds/cone, proportion of seeds with embryos, and proportion of total seeds that were viable for each study site.

Site	Reproductive adults/ha	Cones per tree	Seeds per cone	Seeds with embryos (%)	Viable seeds (%)
1	80	611.54 ± 371.28	29.6 ± 13.68	41.2 ± 18.01	24.2 ± 13.72
2	263	54.46 ± 56.93	40.3 ± 14.90	43.7 ± 20.67	36.6 ± 19.85
3	85	14.03 ± 30.23	31.7 ± 12.95	39.0 ± 17.38	31.1 ± 16.00

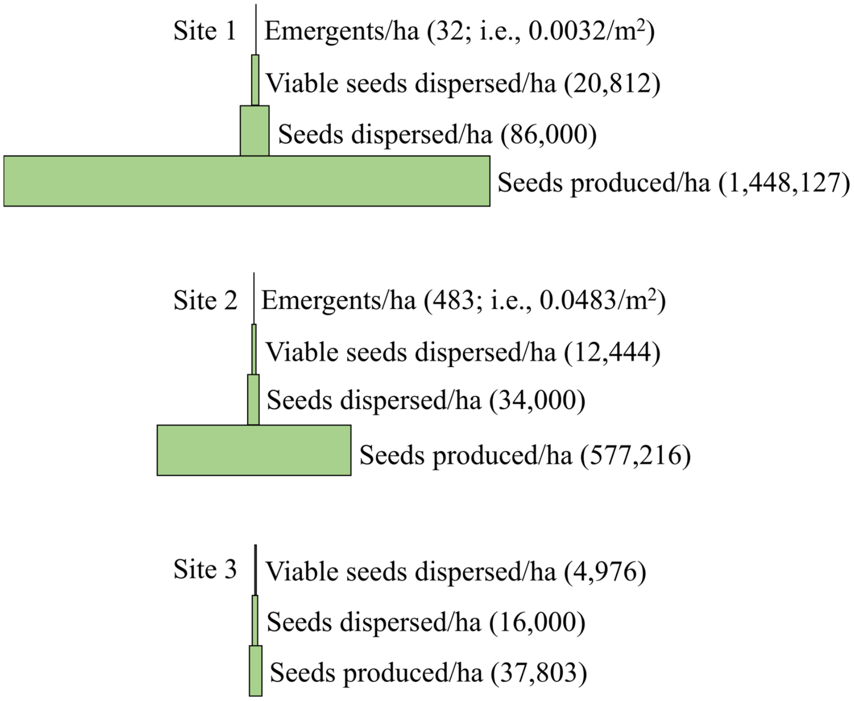


Figure 3.1 Dynamics for the main limiting demographic bottlenecks we identify for black spruce from seed production to germination. Bars show estimated number of seeds or emergents per hectare at each study site. Seeds produced is number of reproductive adults per hectare x mean number of cones per tree x mean number of seeds per cone. Seeds dispersed is the estimated number of seeds dispersed per hectare from seed trap data. Viable seeds dispersed is the number of seeds dispersed per hectare x seed viability. Emergents is the number of viable seeds dispersed x the emergence rate of viable seeds from the seeding experiment. Emergents not shown for Site Three because there was no seeding experiment at this site.

3.4.2 Bottleneck 2: Germination on a suitable microsite

If seed limitations are overcome, we found that few individuals emerged in the field-based seeding experiment and successful emergence decreased towards the range edge (Table 3.2). Black spruce seed emergence occurred in 4/40 and 14/40 experimentally seeded plots at Sites One and Two, respectively. Emergence occurred in 1/80 non-seeded control plots across both sites. In total, Sites One and Two had germination success rates of 0.113% and 3.125%, respectively. The binomial portion of the hurdle model found that the odds of an emergent being present in a seed plot did not change towards the range edge but was significantly more likely to occur in seed addition plots rather than control plots, further suggesting seed availability limitations (Table 3.2). Because only one emergent was found in the 80 control plots, only seeded plots were assessed in the abundance model. In plots with successful emergence, we found abundance decreased towards the range edge (Table 3.2).

Sufficient germination to quantify the emergent niche only occurred at Site Two (see Chapter Two for full NMDS plots of demographic niches). At Site Two, available tundra conditions diverged from emergents towards the range edge for NMDS axis 1, where emergents occupied unique microsites that were dissimilar from the available tundra substrate at the upper end of the transect (Fig. 3.2). Although emergence still occurred at the upper end of the transect, regions of non-overlapping 95% confidence intervals between the two groups indicate emergent microsites were different from the general tundra substrate available (Fig. 3.2).

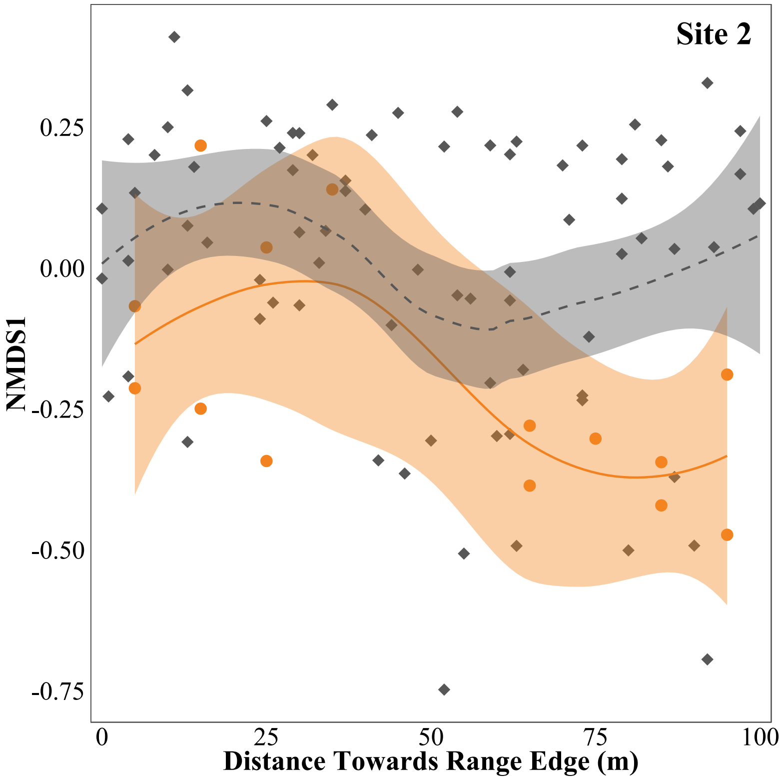


Figure 3.2 Diverging NMDS axis 1 scores towards the range edge for treeless tundra (gray diamonds; dashed line) and emergents (orange circles; solid line) at Site Two (seedling age class shown in Fig. 3.3 and adults in Fig. 3.4). Each point indicates a seed plot with emergents present or a treeless tundra substrate. Distance towards range edge indicates position along the transect. Light shaded region represents 95% confidence intervals for microsite associations. See Supplementary Fig. 3.1 for additional NMDS axes.

3.4.3 Bottlenecks 3-5: Seedling, non-reproductive adult, and reproductive adult microsites

In contrast to the restricted availability of germination microsites and low seed rain, we found seedlings to generally have suitable microsites available across the treeline gradient (Fig. 3.3). Seedling and tundra microsites overlapped for all ordinations except Site One, where microsites diverged for a region of two NMDS axes (Fig. 3.3; Supplementary Fig. 3.2). Adult niche space was different from treeless tundra substrates for the ordination including all sites with non-overlapping 95% confidence intervals in one NMDS axis (Fig. 3.4). Site-specific plots show partial overlap between adults and treeless tundra 95% confidence intervals (Fig. 3.4). Other than short patches of non-overlapping 95% confidence intervals between adult groups for one NMDS axis at Sites One and Two, non-reproductive and reproductive adult microsites were similar to one another (Fig. 3.4).

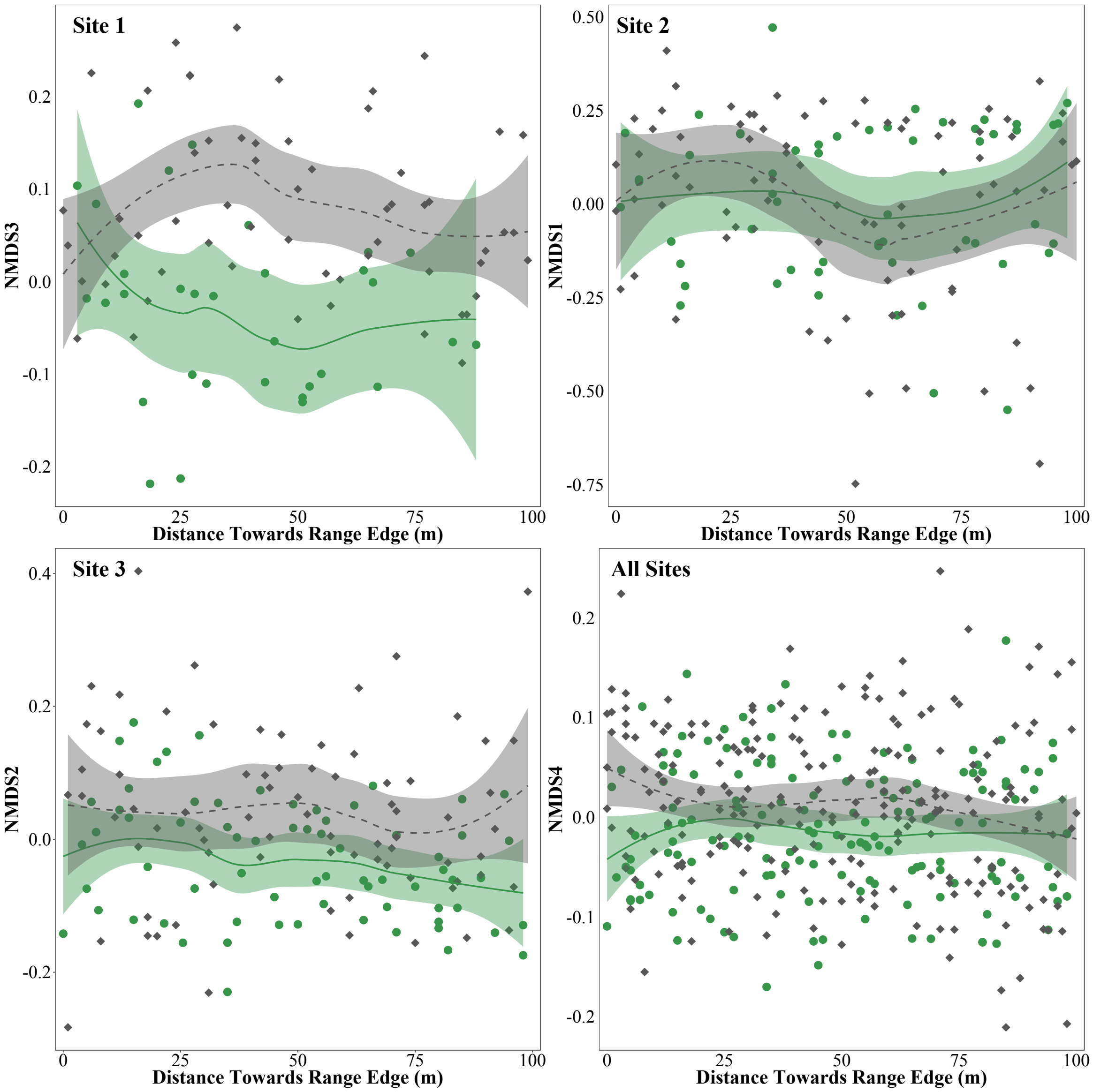


Figure 3.3 Generally overlapping NMDS scores along the treeline gradient for treeless tundra substrates (gray diamonds; dashed line) and seedlings (green circles; solid line) for all three sites separately and all sites combined (note that Site One shows a region of divergence). NMDS axis best showing any divergence between groups shown. Each point indicates an individual or treeless tundra substrate (emergents shown in Fig. 3.2 and adults in Fig. 3.4). Distance towards range edge indicates position along the transect.

Light shaded region represents 95% confidence intervals for microsite associations. See Supplementary Fig. 3.2 for additional NMDS axes.

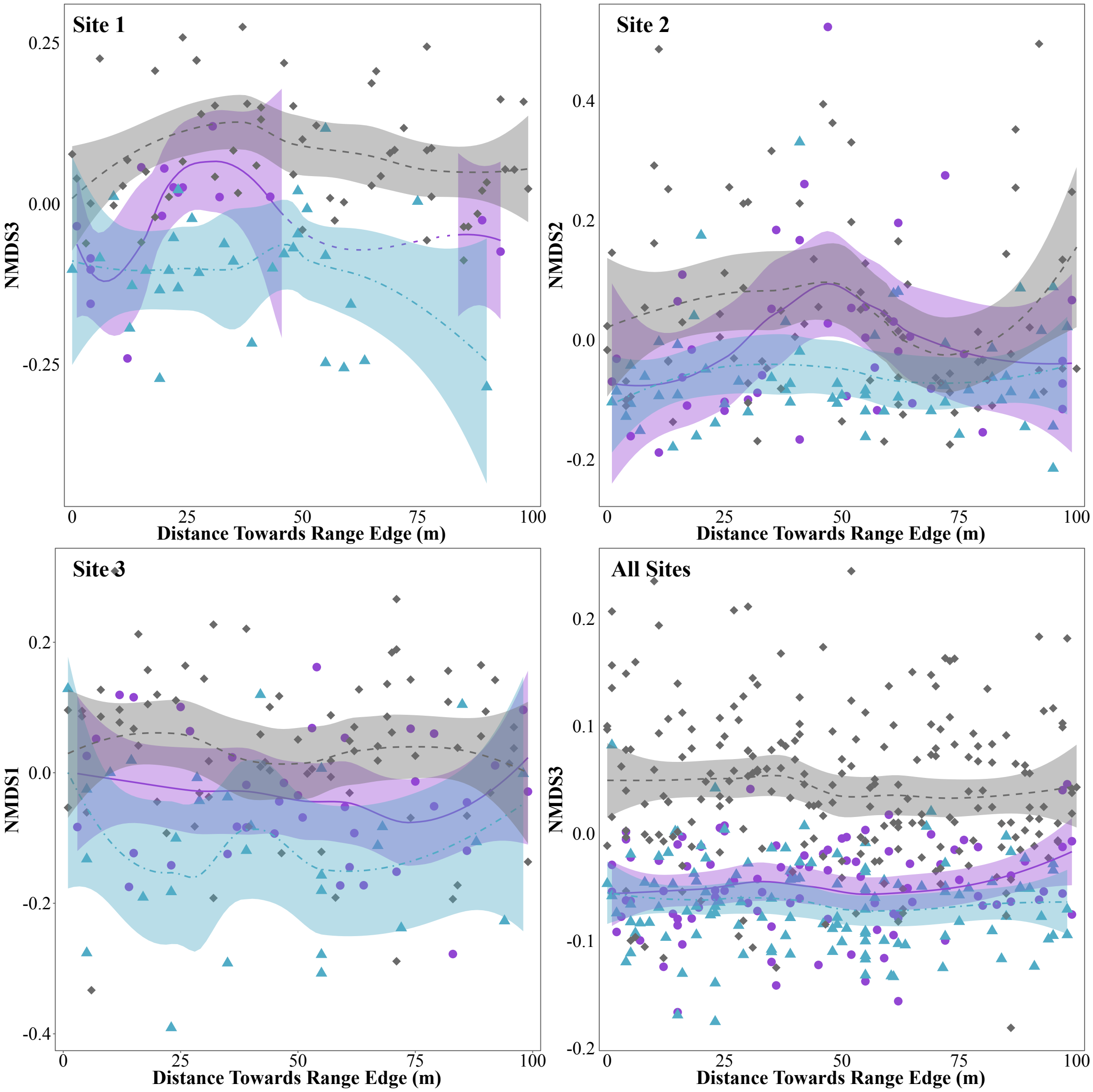


Figure 3.4 Changes in NMDS scores along the treeline gradient for treeless tundra substrates (gray diamonds; dashed line) and adult groups (non-reproductive = purple circles; solid line, reproductive = blue triangles; dotdash line) for all three sites separately

and all sites combined. NMDS axis best showing any divergence between groups shown. Each point indicates an individual or treeless tundra substrate (emergents shown in Fig. 3.2 and seedlings in Fig. 3.3). Distance towards range edge indicates position along the transect. Light shaded region represents 95% confidence intervals for microsite associations. No non-reproductive adults were observed from 43 m to 89 m along transects at Site One. Thus, we do not infer non-reproductive adult niche space in this portion of the ecotone and removed the confidence intervals. See Supplementary Fig. 3.3 for additional NMDS axes.

3.4.4 Microsite changes along the transect

We found treeless tundra substrates to change along our treeline gradient for 5/14 of our microsite variables. Amongst treeless tundra substrates, we found active layer depth, relative light availability, and tall shrub cover decreased towards the range limit (Table 3.4). Additionally, we identified an increase in medium and dwarf shrub cover towards the range limit, and no association between the gradient and the remaining microsite variables measured (Table 3.4).

Table 3.4 Summary of GLMMs comparing changes in microsite variables for tundra substrates with distance towards the range edge as the explanatory variable. Negative values indicate the response declined towards the range edge. Transect nested within site were included as random effects (values not shown). P values significant at the 0.05 level are bolded. N is the sample size for that GLMM as sample sizes varied slightly between microsite variables due to logistical constraints. * indicates a revised p-value from a randomization test due to model assumption violations.

Response Variable	**N**	**Parameter Estimate**	**F value**	**P value**
Soil Moisture (%)	240	0.018	0.663	0.420*
Active Layer Depth (cm)	239	**-0.082**	**7.530**	**0.007**
Soil Organic Layer Depth (cm)	240	0.015	0.908	0.341*
pH	240	-0.0004	0.162	0.687
Soil Temperature 1 (°C)	240	-0.0006	0.020	0.888
Soil Temperature 2 (°C)	240	0.0006	0.061	0.806*
Relative Light Availability	216	**0.001**	**7.113**	**0.009***
Graminoids (% Cover)	240	0.051	2.014	0.152*
Tall Shrubs (% Cover)	240	**-0.059**	**4.044**	**0.044***
Medium Shrubs (% Cover)	240	**0.088**	**5.950**	**0.015**
Dwarf Shrubs (% Cover)	240	**0.086**	**5.902**	**0.016**
Moss (% Cover)	240	-0.077	2.646	0.100*
Lichen (% Cover)	240	0.033	0.525	0.473*
Forbs (% Cover)	240	-0.006	0.085	0.771

3.5 Discussion

Range shifts require suitable conditions to be available throughout a species' life cycle, from seed dispersal to those propagules forming a self-sustaining population. By reconciling demographic niches and changes in microsite availability towards the range edge, we provide empirical evidence that pre-seedling life stages are overwhelmingly the main limiting life stages on climate induced northern black spruce range expansion. Specifically, we found that seed dispersal declined and available niche space for germination became scarce towards the range limit (Fig. 3.1; 3.2). Even if climatic alleviations increase seedling and adult growth and survival, range expansion will be limited until there is an increase in both viable seed availability and suitable germination microsites. Here, we detail microsite availability and demographic patterns leading to early life stage bottlenecks on black spruce range expansion.

3.5.1 Bottleneck 1: Viable seed availability

Range expansion begins with viable seed dispersing beyond the range, a process that we found limiting for northern black spruce populations. Seed rain decreased towards the range edge and was low compared to forest stands (Brown and Johnstone 2012; Rossi et al. 2017) and other treeline populations (Kambo and Danby 2017; but see Hofgaard 1993). Seed rain can vary annually (Roland et al. 2014; Kroiss and HilleRisLambers 2015; Rossi et al. 2017), but higher emergence in seed addition plots than unseeded plots provides further evidence that establishment is limited by viable seed availability. Low seed availability may be related to low stand density at the range edge (Kroiss and

HilleRisLambers 2015; Brown et al. 2019) and associated low cone production. We found cone production did not change towards the range limit, but fewer trees will, inherently, produce less seed than a denser stand. Previous research at these treeline populations (Chapter Two) found black spruce to have a narrow reproduction niche, limiting seed production to a subset of microsites adults occupy. An increase in suitable reproduction niche space may overcome this hurdle and increase seed availability.

Although we did not assess seed viability across the gradient, site level seed viability was lower than southern populations (Sirois 2000; Meunier et al. 2007), but relatively high compared to other treeline populations (Lloyd et al. 2008; Jameson et al. 2015; Brown et al. 2019). At treeline, harsh environmental conditions and low temperatures may reduce seed production and viability (Sveinbjörnsson et al. 2011; Roland et al. 2014; Brown et al. 2019). Additionally, reduced genetic diversity from both low stand density and vegetative reproduction at treeline can lead to self-fertilization and empty seed production or aborted embryos (Owens et al. 2005; O'Connell et al. 2006; Mimura and Aitken 2007). Embryo abortion and empty seed production create unfilled seeds, which we found to be the main cause of non-viable seed production via laboratory germination trials. Overall, our results show that despite viable seed production in our study treeline populations, sufficient seed is not reaching the tundra for range expansion to occur. We suggest the constraining factor within this region may be limited seed quantity, rather than quality.

3.5.2 Bottleneck 2: Germination on a suitable microsite

If seed limitations are alleviated and viable seed successfully disperses beyond the range, seed must land on an appropriate microsite for germination. Low emergence and decreased emergent abundance towards the range edge suggests that germination is another key limiting step for establishment in our black spruce treeline populations. Suitable niche space for emergence was sparse towards the range edge, where the ecological composition of tundra microsites available for colonization diverged from the emergent niche. If sufficient seed successfully reaches these particular microsites, establishment can still happen, barring post-dispersal seed predation (Munier et al. 2010; Kambo and Danby 2017) and unfavourable weather (Zasada et al. 1992; Kullman 2014) which can both filter out potential candidates for establishment. Indeed, an outlier seed plot that exhibited the highest germination (36%) was located closer to the range limit along our treeline gradient. Similar low germination rates have been observed in seed addition experiments for other black spruce treelines (e.g., Wheeler et al. 2011; Crofts and Brown, *in review*). Additionally, decreased emergence towards and beyond the range edge is common (e.g., Hobbie and Chapin 1998; Cuevas 2000; Castanha et al. 2012; but see Frei et al. 2018) and is often limited by microsite availability (Batllori et al. 2009*b*; Dufour-Tremblay et al. 2012; Davis and Gedalof 2018). Decreased emergence may be related to the high ecological inertia of the tundra, where the ecosystem demonstrates a robust ability to resist colonization (Hofgaard and Wilmann 2002). That resistance creates limited niche space for black spruce emergence, which is spatially isolated to select microsites, at least until the inertia is broken via disturbance (e.g., permafrost thaw, fire).

Fires can overcome high inertia of the tundra by removing the plant community and organic layer, temporarily creating altered niche space that favours black spruce germination (e.g., Johnstone and Chapin 2006). If a fire burns across the treeline into the tundra, this process can potentially result in a germination pulse if previously discussed seed limitations are overcome. However, short fire return intervals may limit seed availability (Brown and Johnstone 2012) and scarified substrates at treeline can have increased seed predation (Crofts and Brown, *in review*), suggesting early life stages may still impede range expansion in a post-fire landscape. For pre-seedling bottlenecks to be overcome, annual variation in viable seed production (Sirois 2000; Brown et al. 2019), seed dispersal (Roland et al. 2014; Kroiss and HilleRisLambers 2015), and emergence (Munier et al. 2010; Kullman 2014) must favourably align. Periods of improved seed production and seed rain must precede a good emergence year to saturate the most limiting demographic hurdles we identify here.

3.5.3 Bottleneck 3: Seedling establishment

After germinating, an individual must experience suitable conditions to grow and establish into a seedling, a stage where mortality is high (Germino et al. 2002; Castanha et al. 2012). Available niche space for seedlings generally did not decrease towards the range limit. Suitable substrates for seedlings were available for all ordinations except Site One which had an unsuitable region across the gradient. Our study sites were located in different parts of diffuse treeline ecotone, with different stand densities. Site One was closest to the actual range limit with the lowest stand density and thus may be closer to the seedling niche limit. At Sites Two and Three, our findings suggest that if individuals surpass earlier demographic bottlenecks, then seedling microsite availability does not appear to be a constraining factor on establishment. However, seedlings may still be more susceptible to harsh weather conditions than later stages (Germino et al. 2002; Holtmeier and Broll 2010).

While we did not detect a uniform decline in niche space along the treeline gradient, we did find a region of unsuitable seedling microsite availability at one of our sites (Site One). Along our treeline gradient, active layer depth, light availability, and plant community composition changed, where fewer tall shrubs and more medium and dwarf shrubs were present towards the range limit. Decreased tree abundance has been associated with an increase in medium shrub cover (Trant et al. 2015), but plant community changes across the treeline ecotone are complex and variable (Batllori et al. 2009*a*; Trant et al. 2015). Shrubs have been attributed to have positive effects on seedling establishment (Grace et al. 2002; Renard et al. 2016); yet, in high abundances (>72%), shrubs can limit seedling occurrence (Kambo and Danby 2018) and have a negative effect on seedling establishment (Batllori et al. 2009*b*). The combined effects of multiple microsite variables leads to regions of unsuitable tundra substrates, resulting in non-random spatial associations of seedlings (Batllori et al. 2009*b*; Kambo and Danby 2018) as observed in Site One. Extending this gradient further towards the range limit may capture the limit where combined microsite variables result in completely unsuitable substrates for seedling establishment.

3.5.4 Bottleneck 4: Adult growth and survival

An established seedling must then survive and grow many years into adulthood for a true range shift to occur. Adults appear to be released from microsite limitations for the variables we included. We observed no consistent trend in adult microsite associations, indicating that there were no limitations to where an adult existed across the gradient, from a substrate perspective. Site-specific differences likely reflect the range of tundra conditions available at a given site, where suitable demographic niche space changes in different ways along the gradient. Meanwhile, the wider range of conditions available were captured within the ordination including all three sites. The ordination with all sites showed that adults occupied different microsites from tundra substrates for one NMDS axis. These trends likely reflects adults' ability to alter their microsites (Holtmeier and Broll 2017) by obtaining resources and creating shade. For example, an increase in shade and humidity created by larger adult branches may increase moss cover in adult microsites (Chapter Two; Campeau and Rochefort 1996). This positive feedback can potentially alter a tree's microsite to conditions unique from the tundra substrate it initially colonized. The point at which this occurs remains unclear and would be an enlightening avenue to explore. Additionally, teasing apart the microsite variables that impact adult performance from those that are altered by adults can further elucidate the importance of microsite composition for adult groups. At the adult stage, survival may be more influenced by larger scale factors such as climate (Du et al. 2018) and extreme weather events (Körner 1998; Holtmeier and Broll 2010).

3.5.5 Bottleneck 5: Reproductive maturity and seed production

Once an individual emerges from the understory into the open air, sustained range expansion hinges on established individuals reaching reproductive maturity (Malcolm et al. 2002). For the microsite variables included in the ordinations we present here, non-reproductive and reproductive adult groups occupied similar conditions across all sites. We found no change in reproduction niche availability towards the range edge, yet seed availability decreased. The seed limitations we associated with low seed quantity may be related to low reproductive adult abundance, as discussed above. Decreasing seed availability suggests that we may not have captured the critical part of the reproduction niche that drives viable seed production and becomes limited across the ecotone. Seed production is energetically costly (Lee 1988) and reproductive adults were found to have a narrower niche than their non-reproductive counterpart, which was attributed to a preference for warmer, drier soils with increased nutrient availability (Chapter Two; Hobbie et al. 2002). Assessing the relationship between seed production and nutrient availability towards the range limit may show that suitable niche space for reproduction becomes limited at the range edge, inhibiting range expansion.

3.6 Conclusion

Despite viable seed production at the range edge, we found seed availability to be limited at black spruce treeline. In the event that viable seed successfully disperses, black spruce emergence is limited to a subset of available microsites, which decrease in abundance towards the range edge. Using a multivariate, demographic niche based approach, we show that potential climate induced increases in seed viability (Roland et al. 2014; Brown et al. 2019) and tree growth (Danby and Hik 2007; Ettinger et al. 2011 but see Mamet and Kershaw 2013; Nicklen et al. 2016) will not necessarily result in a range expansion due to stronger regeneration bottlenecks at earlier life stages. Instead, increases in seed quantity and suitable microsite availability for germination will likely alleviate hurdles on black spruce range expansion. Ultimately, expanding and then maintaining a population relies on viable seed reaching a suitable microsite and successively surpassing all demographic bottlenecks through to reproductively mature adults. During this life cycle, a species' ecological requirements may vary (Pironon et al. 2018) and the relative availability of those requirements can change both across the range and amongst microsites within the heterogeneous landscape of a given population. Our technique used here allows for a multivariate understanding of the ecological characteristics and frequency of suitable microsites for establishment across a species' life cycle. Our method can be expanded spatially or temporally to inform how (1) microsite availability; (2) environmental gradients; and (3) the relative intensities of demographic bottlenecks may change across a species' range. Ultimately, this approach can improve our understanding of the role that microsite availability plays on changes in species' distributions under continued climate change.

3.7 References

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Batllori, E., J. M. Bianco-Moreno, J. M. Ninot, E. Gutiérrez, and E. Carrillo. 2009a. Vegetation patterns at the alpine treeline ecotone: The influence of tree cover on abrupt change in species composition of alpine communities. Journal of Vegetation Science 20:814–825.

Batllori, E., J. J. Camarero, J. M. Ninot, and E. Gutiérrez. 2009b. Seedling recruitment, survival and facilitation in alpine Pinus uncinata tree line ecotones. Implications and potential responses to climate warming. Global Ecology and Biogeography 18:460–472.

Black, R. A., and L. C. Bliss. 1980. Reproductive ecology of *Picea mariana* (Mill.) BSP., at tree line near Inuvik, Northwest Territories, Canada. Ecological Monographs 50:331–354.

Brodersen, C. R., M. J. Germino, D. M. Johnson, K. Reinhardt, W. K. Smith, L. M. Resler, M. Y. Bader, et al. 2019. Seedling survival at timberline is critical to conifer mountain forest elevation and extent. Frontiers in Forests and Global Change 2:1–12.

Brown, C. D., G. Dufour-Tremblay, R. G. Jameson, S. D. Mamet, A. J. Trant, X. J. Walker, S. Boudreau, et al. 2019. Reproduction as a bottleneck to treeline advance across the circumarctic forest tundra ecotone. Ecography 43:137–147.

Brown, C. D., and J. F. Johnstone. 2012. Once burned, twice shy: Repeat fires reduce seed availability and alter substrate constraints on Picea mariana regeneration. Forest Ecology and Management 266:34–41.

Brown, C. D., and M. Vellend. 2014. Non-climatic constraints on upper elevational plant range expansion under climate change. Proceedings of the Royal Society B: Biological Sciences 281:1–9.

Camarero, J. J., J. C. Linares, A. I. García-Cervigón, E. Batllori, I. Martínez, and E. Gutiérrez. 2017. Back to the future: The responses of alpine treelines to climate warming are constrained by the current ecotone structure. Ecosystems 20:683–700.

Campeau, S., and L. Rochefort. 1996. *Sphagnum* regeneration on bare peat surfaces: Field and greenhouse experiments. Journal of Applied Ecology 33:599–608.

Caron, G. E., and G. R. Powell. 1989. Patterns of seed-cone and pollen-cone production in young Picea mariana trees. Canadian Journal of Forest Research 19:359–364.

Castanha, C., M. S. Torn, M. J. Germino, B. Weibel, and L. M. Kueppers. 2012. Conifer seedling recruitment across a gradient from forest to alpine tundra: Effects of species, provenance, and site. Plant Ecology & Diversity 6:307–318.

Castanho, C. T., A. A. Oliveira, and P. I. Prado. 2012. The importance of plant life form on spatial associations along a subtropical coastal dune gradient. Journal of Vegetation Science 23:952–961.

Chapin, F. S., M. Sturm, M. C. Serreze, J. P. McFadden, J. R. Key, A. H. Lloyd, A. D. McGuire, et al. 2005. Role of land-surface changes in arctic summer warming. Science 310:657–660.

Cranston, B. H., and L. Hermanutz. 2013. Seed-seedling conflict in conifers as a result of plant-plant interactions at the forest-tundra ecotone. Plant Ecology and Diversity 6:319–327.

Cuevas, J. G. 2000. Tree recruitment at the *Nothofagus pumilio* alpine timberline in Tierra del Fuego, Chile. Journal of Ecology 88:840–855.

Danby, R. K., and D. S. Hik. 2007. Responses of white spruce *(Picea glauca)* to experimental warming at a subarctic alpine treeline. Global Change Biology 13:437–451.

Davis, E. L., and Z. Gedalof. 2018. Limited prospects for future alpine treeline advance in the Canadian Rocky Mountains. Global Change Biology 24:4489–4504.

Donohue, K., R. Rubio de Casas, L. Burghardt, K. Kovach, and C. G. Willis. 2010. Germination, postgermination adaptation, and species ecological ranges. Annual Review of Ecology, Evolution, and Systematics 41:293–319.

Du, H., J. Liu, M.-H. Li, U. Büntgen, Y. Yang, L. Wang, Z. Wu, et al. 2018. Warming-induced upward migration of the alpine treeline in the Changbai Mountains, northeast China. Global Change Biology 24:1256–1266.

Dufour-Tremblay, G., L. De Vriendt, E. Lévesque, and S. Boudreau. 2012. The importance of ecological constraints on the control of multi-species treeline dynamics in Eastern Nunavik, Québec. American Journal of Botany 99:1638–1646.

Environment Canada. 2019. Canadian climate normals 1981-2010 Station Data: Old Crow A.

Eremko, R. D., D. G. W. Edwards, and D. Wallinger. 1989. A guide to collecting cones of British Columbia conifers. Forestry Canada, Victoria, BC.

Eriksson, O., and J. Ehrlén. 1992. Seed and microsite limitation of recruitment in plant populations. Oecologia 91:360–364.

Ettinger, A. K., K. R. Ford, and J. HilleRisLambers. 2011. Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. Ecology 92:1323–1331.

Fraser, J. W. 1976. Viability of Black Spruce Seed in or on a Boreal Forest Seedbed. The Forestry Chronicle 52:229–231.

Freeman, B. G., J. A. Lee-Yaw, J. M. Sunday, and A. L. Hargreaves. 2018. Expanding, shifting and shrinking: The impact of global warming on species' elevational distributions. Global Ecology and Biogeography 27:1268–1276.

Frei, E. R., E. Bianchi, G. Bernareggi, P. Bebi, M. A. Dawes, C. D. Brown, A. J. Trant, et al. 2018. Biotic and abiotic drivers of tree seedling recruitment across an alpine treeline ecotone. Scientific Reports 8:1–12.

Germino, M. J., W. K. Smith, and A. C. Resor. 2002. Conifer seedling distribution and survival in an alpine-treeline ecotone. Plant Ecology 162:157–168.

Grace, J., F. Beringer, and L. Nagy. 2002. Impacts of climate change on the tree line. Annals of Botany 90:537–544.

Harper, J. L. 1977. Population biology of plants. Academic Press Inc., London, U.K.

Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology Letters 12:1040–1049.

Hobbie, S. E., and S. I. Chapin. 1998. An experimental test of limits to tree establishment in arctic tundra. Journal of Ecology 86:446–461.

Hobbie, S. E., K. J. Nadelhoffer, and P. Högberg. 2002. A synthesis: The role of nutrients as constraints on carbon balances in boreal and arctic regions. Plant and Soil 242:163–170.

Hofgaard, A. 1993. Seed rain quantity and quality, 1984–1992, in a high altitude old-growth spruce forest, northern Sweden. New Phytologist 125:635–640.

Hofgaard, A., and B. Wilmann. 2002. Plant distribution pattern across the forest-tundra ecotone: The importance of treeline position. Ecoscience 9:375–385.

Holtmeier, F. K. 2009. Mountain Timberlines: Ecology, Patchiness, and Dynamics. Springer, New York.

Holtmeier, F. K., and G. Broll. 2005. Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. Global Ecology and Biogeography 14:395–410.

Holtmeier, F. K., and G. Broll. 2010. Wind as an ecological agent at treelines in North America, the Alps, and the European subarctic. Physical Geography 31:203–233.

Holtmeier, F. K., and G. Broll. 2017. Feedback effects of clonal groups and tree clusters on site conditions at the treeline: Implications for treeline dynamics. Climate Research 73:85–96.

Jameson, R. G., A. J. Trant, and L. Hermanutz. 2015. Insects can limit seed productivity at the treeline. Canadian Journal of Forest Research 45:286–296.

Johnston, W., and T. Smith. 1985. Black Spruce. Pages 96–98 *in* Silvicultural systems for the major forest types of the United States.

Johnstone, J., L. Boby, E. Tissier, M. Mack, D. Verbyla, and X. Walker. 2009. Postfire seed rain of black spruce, a semiserotinous conifer, in forests of interior Alaska. Canadian Journal of Forest Research 39:1575–1588.

Kambo, D., and R. K. Danby. 2017. Constraints on treeline advance in a warming climate: A test of the reproduction limitation hypothesis. Journal of Plant Ecology 11:411–422.

Kambo, D., and R. K. Danby. 2018. Factors influencing the establishment and growth of tree seedlings at Subarctic alpine treelines. Ecosphere 9:1–17.

Körner, C. 1998. A re-assessment of high elevation treeline positions and their explanation. Oecologia 115:445–459.

Körner, C. 2016. When it gets cold, plant size matters - A comment on treeline. Journal of Vegetation Science 27:6–7.

Krebs, C. J., J. M. LaMontagne, A. J. Kenney, and S. Boutin. 2012. Climatic determinants of white spruce cone crops in the boreal forest of southwestern Yukon. Botany 90:113–119.

Kroiss, S. J., and J. HilleRisLambers. 2015. Recruitment limitation of long-lived conifers: Implications for climate change responses. Ecology 96:1286–1297.

Kullman, L. 2014. Treeline *(Pinus sylvestris)* landscape evolution in the Swedish Scandes – a 40-year demographic effort viewed in a broader temporal context. Norwegian Journal of Geography 68:155–167.

Leadem, C. ., S. L. Gillies, H. K. Yearsley, V. Sit, D. L. Spittlehouse, and P. J. Burton. 1997. Field studies of seed biology. Research Branch B.C. Ministry of Forests, Victoria, BC.

Lee, T. D. 1988. Patterns of fruit and seed production. Pages 179–202 *in* Plant reproductive ecology. Oxford University Press, New York, U.S.A.

Lloyd, A. H., C. L. Fastie, and H. Eisen. 2008. Fire and substrate interact to control the northern range limit of black spruce *(Picea mariana)* in Alaska. Canadian Journal of Forest Research 37:2480–2493.

Malcolm, J. R., A. Markhan, R. P. Neilson, and M. Garaci. 2002. Estimated migration rates under scenarios of global climate change. Journal of Biogeography 29:835–849.

Mamet, S. D., and G. P. Kershaw. 2013. Age-dependency, climate, and environmental controls of recent tree growth trends at subarctic and alpine treelines. Dendrochronologia 31:75–87.

Manley, B. 2006. Randomization, bootstrap and Monte Carlo methods in biology (3rd ed.). Chapman and Hall/CRC.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MJM Software Design, Glenden Beach, Oregon U.S.A.

Meunier, C., L. Sirois, and Y. Begin. 2007. Climate and *Picea Mariana* Seed Maturation Relationships: A Multi-Scale Perspective. Ecological Monographs 77:361–376.

Mimura, M., and S. N. Aitken. 2007. Increased selfing and decreased effective pollen donor number in peripheral relative to central populations in *Picea sitchensis (Pinaceae).* American Journal of Botany 94:991–998.

Moyes, A. B., M. J. Germino, and L. M. Kueppers. 2015. Moisture rivals temperature in limiting photosynthesis by trees establishing beyond their cold-edge range limit under ambient and warmed conditions. New Phytologist 207:1005–1014.

Munier, A., L. Hermanutz, J. D. Jacobs, and K. Lewis. 2010. The interacting effects of temperature, ground disturbance, and herbivory on seedling establishment: Implications for treeline advance with climate warming. Plant Ecology 210:19–30.

Nicklen, F. E., C. A. Roland, R. W. Ruess, J. H. Schmidt, and A. H. Lloyd. 2016. Local site conditions drive climate-growth responses of *Picea mariana* and *Picea glauca* in interior Alaska. Ecosphere 7:1–17.

O'Connell, L. M., A. Mosseler, and O. P. Rajora. 2006. Impacts of forest fragmentation on the reproductive success of white spruce *(Picea glauca).* Canadian Journal of Botany 84:956–965.

Oksanen, J., F. Guillaume-Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, et al. 2013. “Vegan” community ecology package.

Owens, J. N., J. Bennett, and S. L’Hirondelle. 2005. Pollination and cone morphology affect cone and seed production in lodgepole pine seed orchards. Canadian Journal of Forest Research 35:383–400.

Pepin, N., R. S. Bradley, H. F. Diaz, M. Baraer, E. B. Caceres, N. Forsythe, H. Fowler, et al. 2015. Elevation-dependent warming in mountain regions of the world. Nature Climate Change 5:424–430.

Pironon, S., J. Villellas, W. Thuiller, V. M. Eckhart, M. A. Geber, D. A. Moeller, and M. B. García. 2018. The “Hutchinsonian niche” as an assemblage of demographic niches: Implications for species geographic ranges. Ecography 41:1103–1113.

Quero, J. L., L. Gómez-Aparico, R. Zamora, and F. T. Maestre. 2008. Shifts in the regeneration niche of an endangered tree *(Acer opalus ssp. granatense)* during ontogeny: Using an ecological concept for application. Basic and Applied Ecology 9:635–644.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Renard, S. M., E. J. B. McIntire, and A. Fajardo. 2016. Winter conditions - not summer temperature - influence establishment of seedlings at white spruce alpine treeline in Eastern Quebec. Journal of Vegetation Science 27:29–39.

Resler, L., D. Butler, and G. Malanson. 2005. Topographic shelter and conifer establishment and mortality in an alpine environment, Glacier National Park, Montana. Physical Geography 26:112–125.

Roland, C. A., J. H. Schmidt, and J. F. Johnstone. 2014. Climate sensitivity of reproduction in a mast-seeding boreal conifer across its distributional range from lowland to treeline forests. Oecologia 174:665–677.

Rossi, S., H. Morin, F. Gionest, and D. Laprise. 2017. Inter-and intra-annual patterns of seed rain in the black spruce stands of Quebec, Canada. IForest 10:189–195.

Safford, L. O. 1974. Picea A. Dietr. Spruce. Pages 587–596 *in* Seeds of woody plants in the United States. Washington, D.C.

Schurr, F. M., J. Pagel, J. S. Cabral, J. Groeneveld, O. Bykova, R. B. O'Hara, F. Hartig, et al. 2012. How to understand species' niches and range dynamics: A demographic research agenda for biogeography. Journal of Biogeography 39:2146–2162.

Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of species range limits. Annual Review of Ecology, Evolution, and Systematics 40:415–436.

Sirois, L. 2000. Spatiotemporal variation in black spruce cone and seed crops along a boreal forest - tree line transect. Canadian Journal of Forest Research 30:900–909.

Smith, C., J. Meikle, and C. Roots. 2004. Ecoregions of the Yukon Territory: Biophysical Properties of Yukon Landscapes. Summerland, BC.

Sullivan, P. F., and B. Sveinbjörnsson. 2010. Microtopographic control of treeline advance in Noatak National Preserve, Northwest Alaska. Ecosystems 13:275–285.

Sveinbjörnsson, B., A. Hofgaard, and A. Lloyd. 2011. Natural causes of the tundra-taiga boundary. Interface Ambio:23–29.

Tarnocai, C., C. A. S. Smith, and C. A. Fox. 1993. International tour of permafrost affected soils: The Yukon and Northwest Territories of Canada. Ottawa.

Trant, A. J., R. G. Jameson, and L. Hermanutz. 2011. Persistence at the tree line: Old trees as opportunists. Arctic 64:367–370.

Trant, A. J., K. Lewis, B. H. Cranston, J. A. Wheeler, R. G. Jameson, J. D. Jacobs, L. Hermanutz, et al. 2015. Complex changes in plant communities across a subarctic alpine tree line in Labrador, Canada. Arctic 68:500–512.

Viglas, J. N., C. D. Brown, and J. F. Johnstone. 2013. Age and size effects on seed productivity of northern black spruce. Canadian Journal of Forest Research 43:534–543.

Walker, X., G. H. R. Henry, K. McLeod, and A. Hofgaard. 2012. Reproduction and seedling establishment of *Picea glauca* across the northernmost forest-tundra region in Canada. Global Change Biology 18:3202–3211.

Wang, Y., N. Pederson, A. M. Ellison, H. L. Buckley, B. S. Case, E. Liang, and J. J. Camarero. 2016. Increased stem density and competition may diminish the positive effects of warming at alpine treeline. Ecology 97:1668–1679.

Wheeler, J. A., L. Hermanutz, and P. M. Marino. 2011. Feathermoss seedbeds facilitate black spruce seedling recruitment in the forest-tundra ecotone (Labrador, Canada). Oikos 120:1263–1271.

Wickham, H., W. Chang, L. Henry, T. Lin Pederson, K. Takahaski, C. WIlke, and K. Woo. 2016. ggplot2: Elegant graphics for data analysis. Springer-Verlag New York.

Wilson, C., J. Grace, S. Allen, and F. Slack. 1987. Temperature and stature: A study of temperatures in montane vegetation. Functional Ecology 1:405–413.

Zasada, J. C., T. L. Sharik, and M. Nygren. 1992. The reproductive process in boreal forests. Pages 95–135 *in* A systems analysis of the global boreal forest. Cambridge University Press, Cambridge, U.K.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions into ecology with R. New York, NY: Spring Science and Business Media.

Chapter 4: Summary and conclusions

Species are expected to shift their ranges northward or to higher elevations under continued climate change (Chen et al. 2011). The most intense climate warming is happening in northern latitudes (Chapin et al. 2005; Johannessen et al. 2016) where the upper range limit for many boreal tree species occurs (i.e., treeline). Therefore, treelines create an excellent model system to examine the relative importance of the factors that shape a species' range under contemporary climate change. Despite climate warming, species' range shifts have been inconsistent, both globally and at treeline (e.g., Harsch et al. 2009; Henry et al. 2012; Freeman et al. 2018), highlighting the need to explore non-climatic factors that alter predicted climate-induced range shifts.

Throughout a species' life cycle, demographic processes will sequentially filter out candidates for establishment. If suitable conditions are absent or scarce beyond the range for any life stage, a regeneration bottleneck will occur. Comparing constraints on range expansion throughout a species' life cycle will identify which life stage(s) are most limiting and what environmental factors constrain those stages. This demographic view informs the circumstances under which a range shift will likely occur. Such life stage specific constraints on range expansion can be viewed through the lens of demographic niches. This approach divides a species' Hutchinson niche demographically, where each life stage has unique niche dimensions forming multiple demographic niches (Hutchinson 1957; Maquire 1973; Pironon et al. 2018). Changes in demographic niche breadth throughout the life cycle are known as ontogenetic niche shifts (Parrish and Bazzaz 1985).

Life stages with either the narrowest demographic niche breadth, or the least available niche space at and beyond the range limit, will be a rate-limiting step for climate-induced range expansion. In this thesis, I presented a novel approach to understanding demographic hurdles on climate-induced range expansion. I characterized demographic niches for sub-arctic black spruce (*Picea mariana*) populations in the Yukon to identify demographic bottlenecks in both niche breadth (Chapter Two) and available niche space at the range edge (Chapter Three). To achieve this, I quantified individual tree microsites inhabited by different life stages of black spruce along a treeline gradient heading towards the range edge. The breadth of conditions occupied by different life stages formed black spruces' demographic niches (Chapter Two). Then, I compared microsites inhabited by individuals with unoccupied treeless tundra substrates to assess changes in available niche space towards the range edge (Chapter Three). I also quantified seed availability and germination rates along the treeline gradient to further identify the relative importance of demographic processes in hindering northern range expansion (Chapter Three).

4.1 Key findings and future research directions

My results show that northern black spruce populations exhibited shifting demographic niches and microsite preferences throughout the life cycle. I found that demographic patterns changed along the treeline gradient heading towards the range edge, creating regeneration bottlenecks on range expansion. Here, I discuss the key demographic patterns I identified throughout the life cycle and propose future research directions inspired by my findings.

Dispersal of viable seed beyond the range is the initial demographic hurdle to overcome. I found viable seed was produced in my study region, but seed rain was low and decreased towards the range edge (Chapter Three). This suggests the area is more limited by seed quantity than seed quality. Thus, seed availability is a key limiting step in range expansion, as observed across the circumpolar treeline (Brown et al. 2019). To overcome this bottleneck, an increase in available reproduction niche space would increase stand density of reproductively mature adults and increase seed quantity (Kroiss and HilleRisLambers 2015).

If seed limitations are overcome, dispersed seed must land on a suitable substrate for germination for range expansion to occur. Black spruce had a narrow emergent niche (Chapter Two), and available niche space became restricted towards the range edge (Chapter Three). My findings provide further evidence that emergence is an overwhelmingly limiting demographic bottleneck on treeline advance (e.g., Wheeler et al. 2011; Dufour-Tremblay et al. 2012). An important thing to consider for regeneration is that systems change over time; fires will alter the substrate and change available niche space. As a semi-serotinous species, black spruce is known to favourably germinate on temporarily available post-fire niche space (e.g., Brown and Johnstone 2012; Veilleux-Nolin and Payette 2012). Thus, the emergent bottleneck may be overcome if a fire burns across the treeline into the tundra, creating suitable emergent niche space that did not exist in the tundra’s undisturbed state. Given rapidly changing fire regimes observed globally (Flannigan et al. 2009) and increasing fire activity in tundra ecosystems (Hu et al. 2010), considering both undisturbed and disturbed regions when characterizing regeneration niches will provide a more comprehensive understanding of the species’ response to climate change.

Transitioning from emergent to seedling, I identified a shifting and expanding niche breadth (Chapter Two). Overall, seedlings had the broadest niche of all life stages (Chapter Two), and available niche space did not decrease towards the range edge (Chapter Three) demonstrating that seedlings may not be as limiting as earlier regeneration bottlenecks. Despite their broad niche, seedlings exhibited microsite preferences, indicating non-random spatial associations at treeline as observed elsewhere (e.g., Batllori et al. 2009; Kambo and Danby 2018). Seedling niche space was restricted for regions at Site One, which had the lowest stand density and was closest to the range edge. I hypothesize that the seedling niche limit lies further into the tundra ecosystem, which was inaccessible at my study sites.

Progressing from a seedling to a non-reproductive adult, I identified a directionally shifting and contracting niche breadth (Chapter Two). Non-overlapping niche space suggests many seedlings at the range edge currently occupy unsuitable conditions for adulthood, forming an additional limiting bottleneck. I found adults were not limited by microsite availability for the variables included in this study (Chapter Three). Additionally, regions of niche space occupied exclusively by adult groups suggest that adults alter their own microsites. This process is an example of the niche as a function (Elton 1927), as opposed to a species' requirements (Grinnell 1922; Hutchinson 1957), where the species themselves impact microsite variables (e.g., moss cover as described in Chapter Two). This Eltonian niche view complicates the ability to identify suitable habitat for a species. Chase and Leibold (2003) proposed a unified definition where the niche is both the range of environmental conditions in which a species can survive and the effects that a species has on those environmental conditions. In turn, this revised niche definition can be incorporated into our understanding of species' distributions, where the Hutchinson niche is separated into two classes: Grinellian variables that the species will not change and Eltonian variables that are impacted by the species (Soberón 2007). Considering Eltoninian niche theory can inform how treeline advance will, in turn, effect the invaded tundra ecosystem as trees alter their microsites.

Between non-reproductive and reproductive adults, a niche contraction occurred (Chapter Two). Black spruce's narrow reproduction niche suggests that seed production will be limited where suitable niche space is unavailable, forming non-reproductive sink populations and impeding sustained range expansion. I found no change in reproduction microsite availability towards the range edge (Chapter Three); however, decreasing seed availability towards the range edge suggests that I may not have captured crucial microsite variables that drive seed production and become limited across the ecotone. I hypothesize that low seed availability may be driven by limited nutrient availability. In my study region, which is characterized by wet soils and continuous permafrost, reproductive adults preferred warmer, drier microsites that likely have a higher nutrient turnover (Chapter Two; Hobbie et al. 2002). Seed production may then require relatively high nutrient availability. Research has looked at nutrients and seedling establishment at treeline (Sullivan and Sveinbjörnsson 2010; Davis et al. 2018), but the role of nutrients in sexual reproduction at treeline remains unclear. Soil nutrient levels were intended to be included as microsite variables in niche analyses for this thesis. Regrettably, soil grabs to capture nutrients at the microsite level proved impractical at my sites, where organic matter composed most of the underlying substrate and obtaining sufficient soil was not feasible.

4.2 Study limitations

The main limitation of my research is the dimension of time. Microsites were measured for individuals in a single growing season. Space-for-time substitutions are a well-established practice when long term monitoring is not feasible (i.e., treeline species have a long life span) (Pickett 1989). However, as I discuss throughout this thesis, the microsite an individual inhabits can change over time. I can definitively say that a given life stage can occur within the niche space I observed them in; however, we cannot know the conditions in which individuals originally established or how they will fare in their microsites as they age. Furthermore, annual climate variation can change the available niche space for early establishment. For example, we found more germination occurred on moist substrates. Therefore, there may be more available emergent niche space in wetter summers than drier summers. Long term monitoring of individuals occupying a range of microsites would provide a more complete understanding of ontogenetic niche shifts. My approach informs what microsite variables to explicitly test in these studies (i.e., variables driving niche shifts as summarized in Fig. 2.5; nutrient availability as described above).

4.3 Conclusion

Demographic processes will sequentially eliminate candidates for establishment beyond the range throughout a species' life cycle. By comparing demographic niches to available tundra substrates, I found that narrow emergent and reproduction niches (resulting in low seed availability) are the two main limiting bottlenecks for northern black spruce range expansion in subarctic Yukon. Niche space was generally available for seedlings and adults across my treeline gradient, but I found that many seedlings occupy conditions that are unsuitable for adults. Overall, I have demonstrated that demographic niches can inform how species' range dynamics are influenced by life stage-specific requirements and microsite availability. This approach can be expanded to ask essential questions about species' distributions across the range of a population or species. For example, demographic niches can reconcile discrepancies between niche limits and range limits caused by source-sink dynamics (Pulliam 2000) through considering non-reproductive and reproductive niches separately. Additionally, ontogenetic niche shifts can inform whether early life stages observed beyond the range occupy conditions suitable for adulthood, strengthening range shift predictions (Máliš et al. 2016). Ultimately, this novel approach can provide valuable contributions towards understanding how species' distributions and abundances will respond to climate change.

4.4 References

Batllori, E., J. J. Camarero, J. M. Ninot, and E. Gutiérrez. 2009. Seedling recruitment, survival and facilitation in alpine Pinus uncinata tree line ecotones. Implications and potential responses to climate warming. Global Ecology and Biogeography 18:460–472.

Brown, C. D., G. Dufour-Tremblay, R. G. Jameson, S. D. Mamet, A. J. Trant, X. J. Walker, S. Boudreau, et al. 2019. Reproduction as a bottleneck to treeline advance across the circumarctic forest tundra ecotone. Ecography 43:137–147.

Brown, C. D., and J. F. Johnstone. 2012. Once burned, twice shy: Repeat fires reduce seed availability and alter substrate constraints on Picea mariana regeneration. Forest Ecology and Management 266:34–41.

Chapin, F. S., M. Sturm, M. C. Serreze, J. P. McFadden, J. R. Key, A. H. Lloyd, A. D. McGuire, et al. 2005. Role of land-surface changes in arctic summer warming. Science 310:657–660.

Chase, J. M., and M. A. Leibold. 2003. Ecological niches: linking classical and contemporary approaches. The University of Chicago Press, Chicago, U.S.A.

Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026.

Davis, E. L., H. A. Hager, and Z. Gedalof. 2018. Soil properties as constraints to seedling regeneration beyond alpine treelines in the Canadian Rocky Mountains. Arctic, Antarctic, and Alpine Research 50:1–15.

Dufour-Tremblay, G., L. De Vriendt, E. Lévesque, and S. Boudreau. 2012. The importance of ecological constraints on the control of multi-species treeline dynamics in Eastern Nunavik, Québec. American Journal of Botany 99:1638–1646.

Elton, C. 1927. Niches. Pages 63–69 inAnimal Ecology.

Flannigan, M. D., M. A. Krawchuk, W. J. de Groot, B. M. Wotton, and L. M. Gowman. 2009. Implications of changing climate for global wildland fire. International Journal of Wildland Fire 18:483.

Freeman, B. G., J. A. Lee-Yaw, J. M. Sunday, and A. L. Hargreaves. 2018. Expanding, shifting and shrinking: The impact of global warming on species' elevational distributions. Global Ecology and Biogeography 27:1268–1276.

Grinnell, J. 1922. The role of the "accidental." The Auk 39:373–380.

Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology Letters 12:1040–1049.

Henry, G. H. R., K. A. Harper, W. Chen, J. R. Deslippe, R. F. Grant, P. M. Lafleur, E. Lévesque, et al. 2012. Effects of observed and experimental climate change on terrestrial ecosystems in northern Canada:Results from the Canadian IPY program. Climatic Change 115:207–234.

Hobbie, S. E., K. J. Nadelhoffer, and P. Högberg. 2002. A synthesis: The role of nutrients as constraints on carbon balances in boreal and arctic regions. Plant and Soil 242:163–170.

Hu, F. S., P. E. Higuera, J. E. Walsh, W. L. Chapman, P. A. Duffy, L. B. Brubaker, and M. L. Chipman. 2010. Tundra burning in Alaska: Linkages to climatic change and sea ice retreat. Journal of Geophysical Research: Biogeosciences 115:1–8.

Hutchinson, G. E. 1957. Concluding Remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427.

Johannessen, O. M., S. I. Kuzmina, L. P. Bobylev, and M. Myles. 2016. Surface air temperature variability and trends in the Arctic: New amplification assessment and regionalisation. Tellus A: Dynamic Meteorology and Oceanography 68:1–12.

Kambo, D., and R. K. Danby. 2018. Factors influencing the establishment and growth of tree seedlings at Subarctic alpine treelines. Ecosphere 9:1–17.

Kroiss, S. J., and J. HilleRisLambers. 2015. Recruitment limitation of long-lived conifers: Implications for climate change responses. Ecology 96:1286–1297.

Máliš, F., M. Kopecký, P. Petřík, J. Vladovič, J. Merganič, and T. Vida. 2016. Life stage, not climate change, explains observed tree range shifts. Global Change Biology

22:1904–1914.

Maquire, B. J. 1973. Niche Response Structure and the Analytical Potentials of Its Relationship to the Habitat. The American Naturalist 107:213–246.

Parrish, J. A. D., and F. A. Bazzaz. 1985. Ontogenetic niche shifts in old-field annuals. Ecology 66:1296–1302.

Pickett, S. T. 1989. Space-for-time substitution as an alternative to long-term studies. Pages 110–135 inLong-term studies in ecology: Approaches and alternatives. Springer, New York, U.S.A.

Pironon, S., J. Villellas, W. Thuiller, V. M. Eckhart, M. A. Geber, D. A. Moeller, and M. B. García. 2018. The “Hutchinsonian niche” as an assemblage of demographic niches: Implications for species geographic ranges. Ecography 41:1103–1113.

Pulliam, H. R. 2000. On the relationship between niche and distribution. Ecology Letters 3:349–361.

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. Ecology Letters 10:1115–1123.

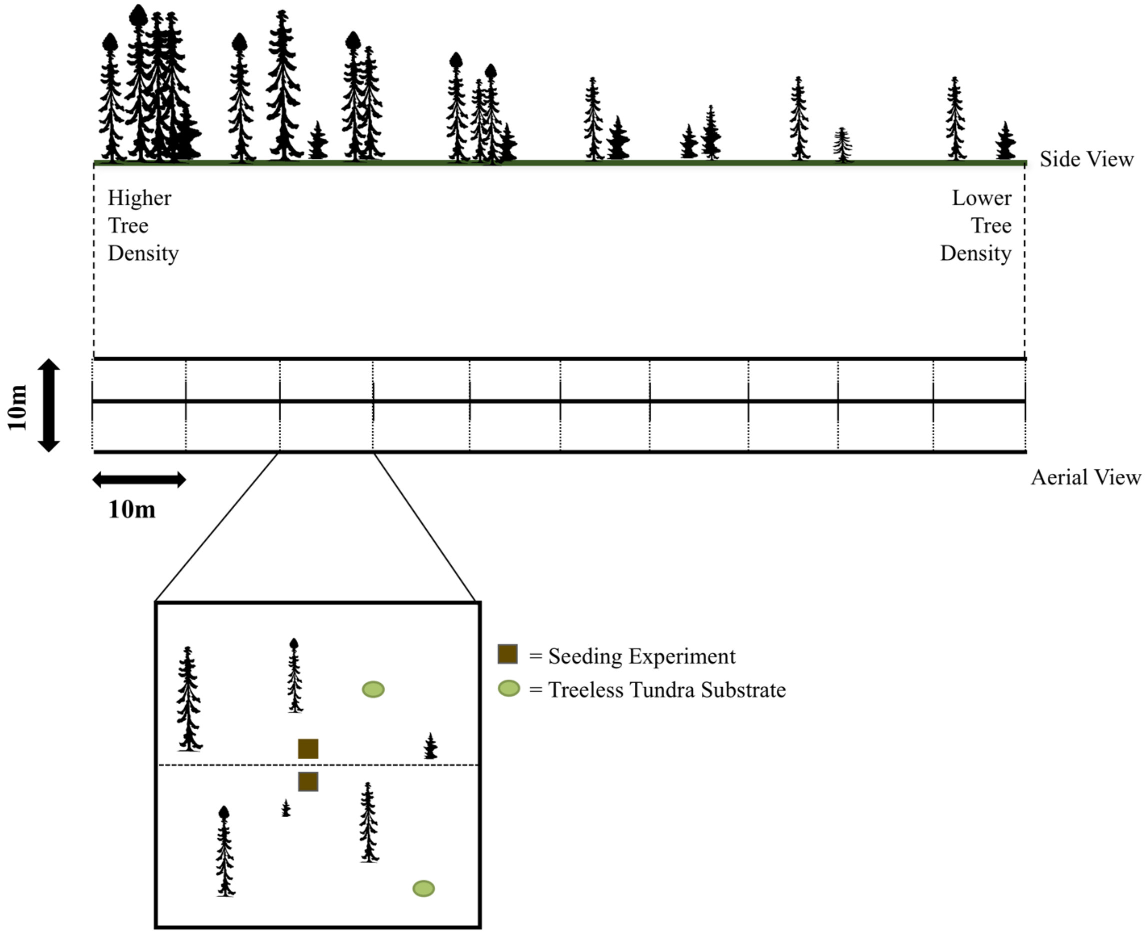
Sullivan, P. F., and B. Sveinbjörnsson. 2010. Microtopographic control of treeline advance in Noatak National Preserve, Northwest Alaska. Ecosystems 13:275–285.

Veilleux-Nolin, M., and S. Payette. 2012. Influence of recent fire season and severity on black spruce regeneration in spruce – moss forests of Quebec, Canada. Canadian

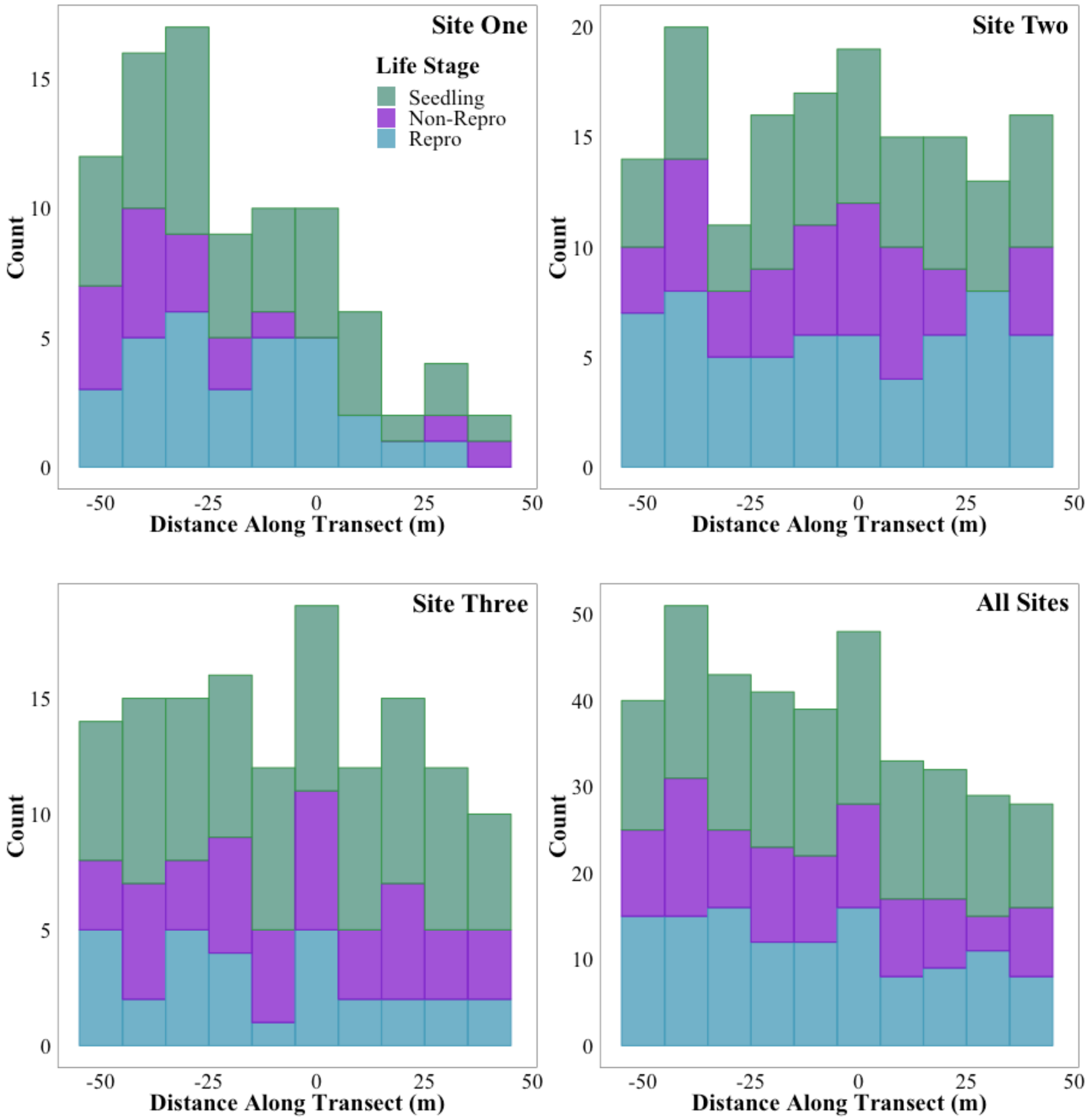
Journal of Forest Research 42:1316–1327.

Wheeler, J. A., L. Hermanutz, and P. M. Marino. 2011. Feathermoss seedbeds facilitate black spruce seedling recruitment in the forest-tundra ecotone (Labrador, Canada). Oikos 120:1263–1271.

Supplementary Materials



Supplementary Figure 2.1 Diagram of site design for this study. The top portion is an aerial and side view of a 100 m x 10 m transect passing through treeline. Dashed lines represent the 10 m increments within which a pair of seed plots were established and up to two seedlings, non-reproductive adults, reproductive adults and treeless tundra substrates were marked for microsite characterization.



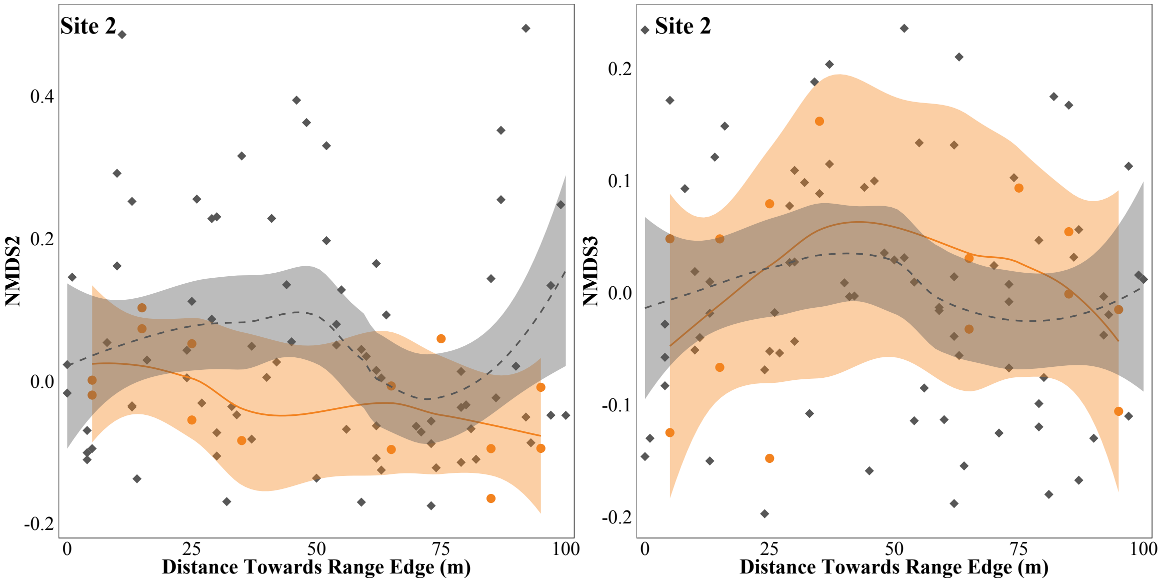
Supplementary Figure 2.2 Stacked histograms showing the distribution of individuals included in this study along transects for each site.

Supplementary Table 2.1 Site breakdown of the number of individuals of each life stage

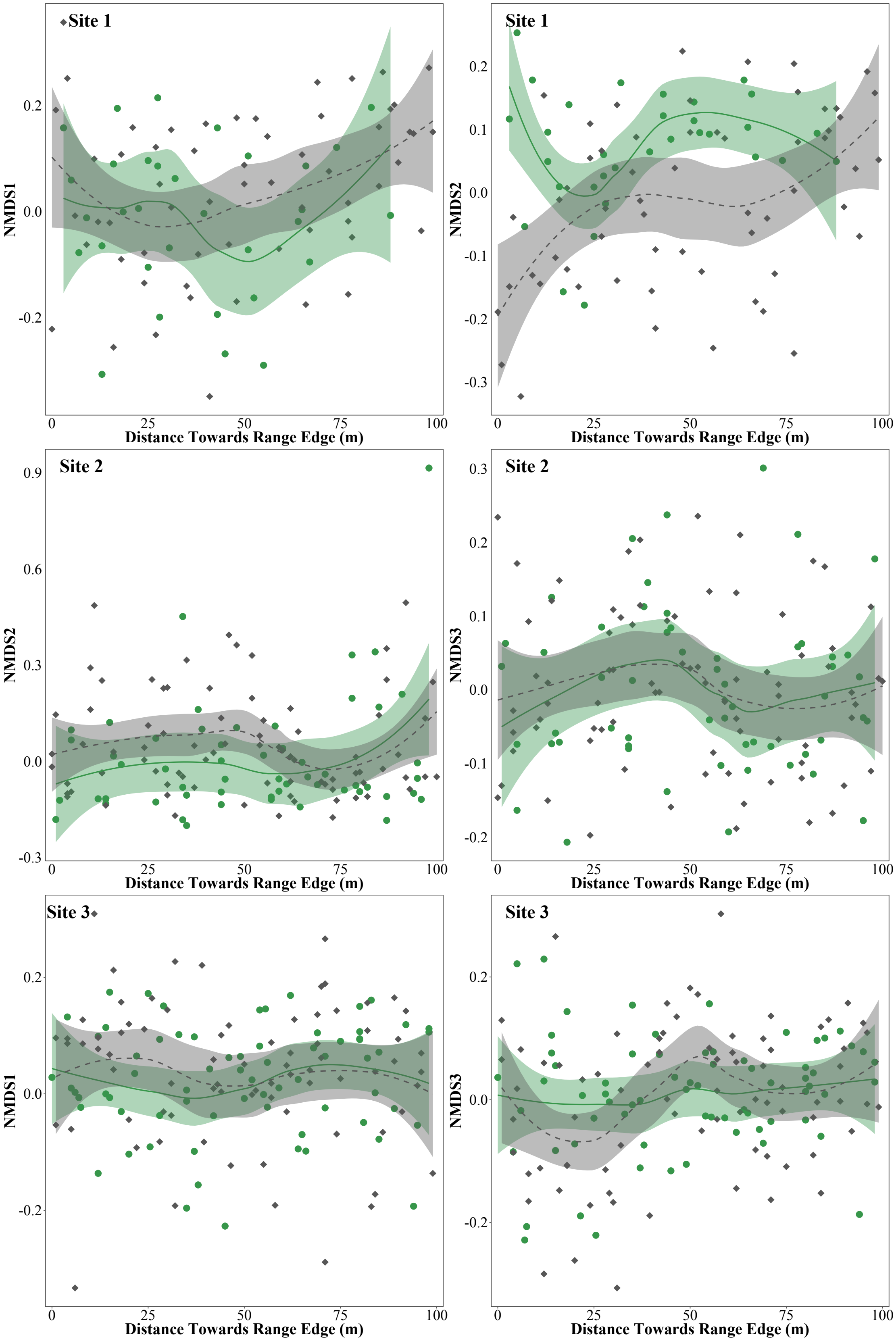
Site	Emergents	Seedlings	Non-Repro	Repro
One	N/A	40	17	31
Two	14	55	40	61
Three	N/A	70	40	30
All	N/A	165	97	122

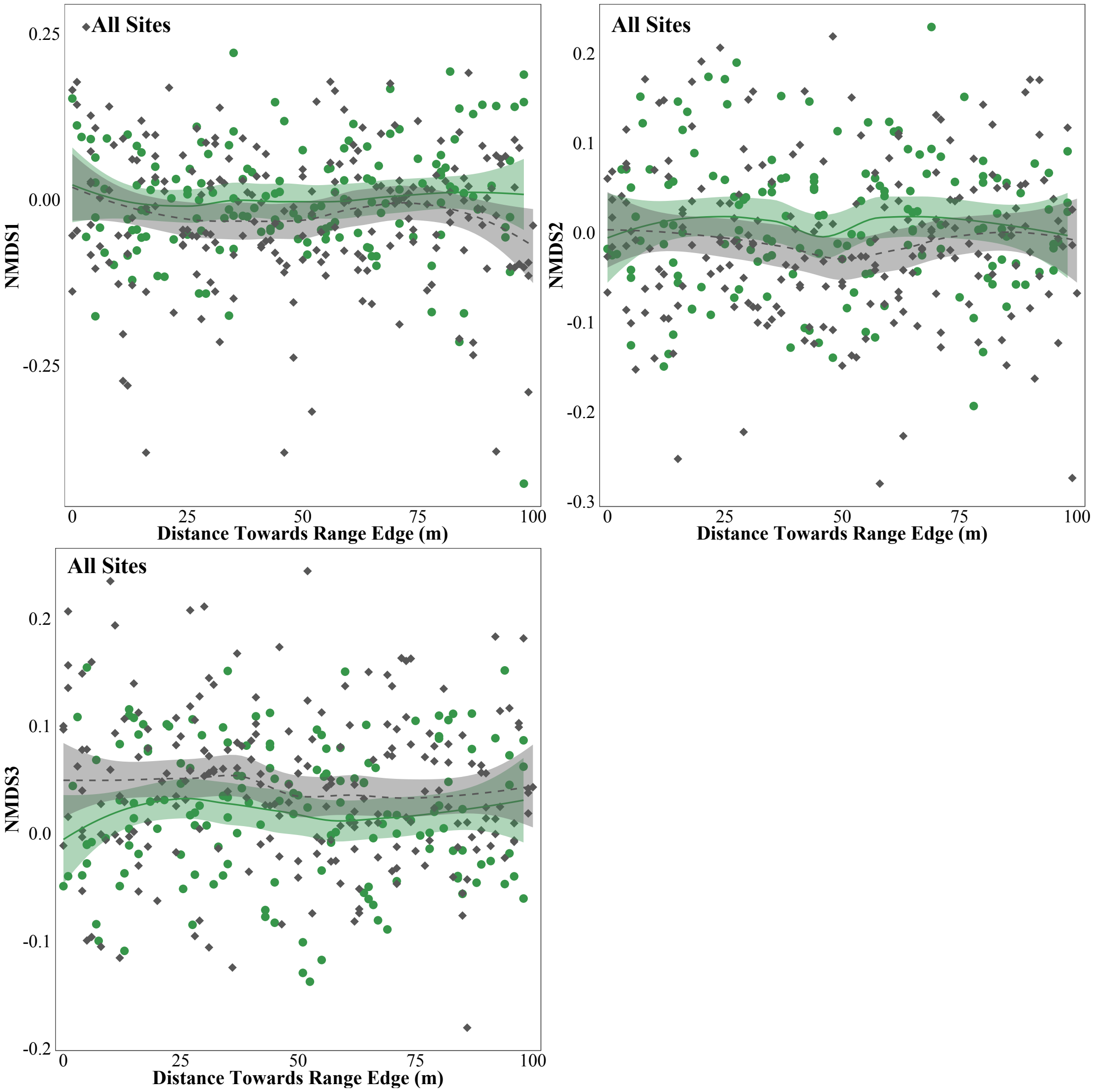
Supplementary Table 2.2 Tukey's HSD Post Hoc test results identifying significant differences in group means from significantly different GLMMs comparing microsite variable differences between life stages with transect nested within site as a random effect (Table 3). TT = treeless tundra, S = seedlings, NR = Non-Reproductive Adults, R = Reproductive Adults. Emergents are not included because their niche was only quantified at one site; results are reported in text. Bolded values indicate statistically significant difference at the 0.05 level.

	TT-S		**TT-NR**		**TT-R**		**S-NR**		**S-R**		**NR-R**	
Variable	**t-ratio**	**p**	**t-ratio**	**p**	**t-ratio**	**p**	**t-ratio**	**p**	**t-ratio**	**p**	**t-ratio**	**p**
Soil Organic Layer Depth (cm)	-1.035	0.729	-0.411	0.976	2.457	0.068	0.429	0.973	**3.153**	**0.009**	-2.371	0.084
Soil Moisture (%)	-1.089	0.696	-0.188	0.997	**-3.403**	**0.004**	1.041	0.725	-2.25	0.111	**-2.955**	**0.017**
Soil Temperature 2 (°C)	-0.632	0.923	0.359	0.984	**2.671**	**0.039**	0.840	0.835	**3.011**	**0.014**	-1.872	0.241
Relative Light Availability	**3.062**	**0.012**	**11.404**	**<0.001**	**13.390**	**<0.001**	**8.349**	**<0.001**	**9.841**	**<0.001**	-0.986	0.757
Tall Shrubs (% Cover)	**-4.802**	**<0.001**	**-4.955**	**<0.001**	**-7.893**	**<0.001**	-0.881	0.814	**-3.303**	**0.006**	2.090	0.157
Medium Shrubs (% Cover)	0.362	0.717	1.392	0.492	**5.672**	**<0.001**	1.027	0.608	**4.969**	**<0.001**	**-3.416**	**0.002**
Dwarf Shrubs (% Cover)	**4.283**	**<0.001**	**3.519**	**0.003**	0.655	0.914	-0.064	0.999	**-2.980**	**0.016**	2.572	0.051
Graminoids (% Cover)	**-2.817**	**0.026**	-0.984	0.759	-1.744	0.302	1.303	0.561	0.742	0.880	0.561	0.944
Moss (% Cover)	0.984	0.759	1.107	0.685	**3.366**	**0.004**	0.267	0.993	2.302	0.099	-1.781	0.284
Lichen (% Cover)	**-2.930**	**0.018**	-2.451	0.069	**-4.762**	**<0.001**	0.005	0.999	-1.966	0.202	1.739	0.304
Forbs (% Cover)	0.916	0.796	-2.366	0.085	-1.979	0.197	**-2.964**	**0.017**	**-2.608**	**0.046**	-0.467	0.966

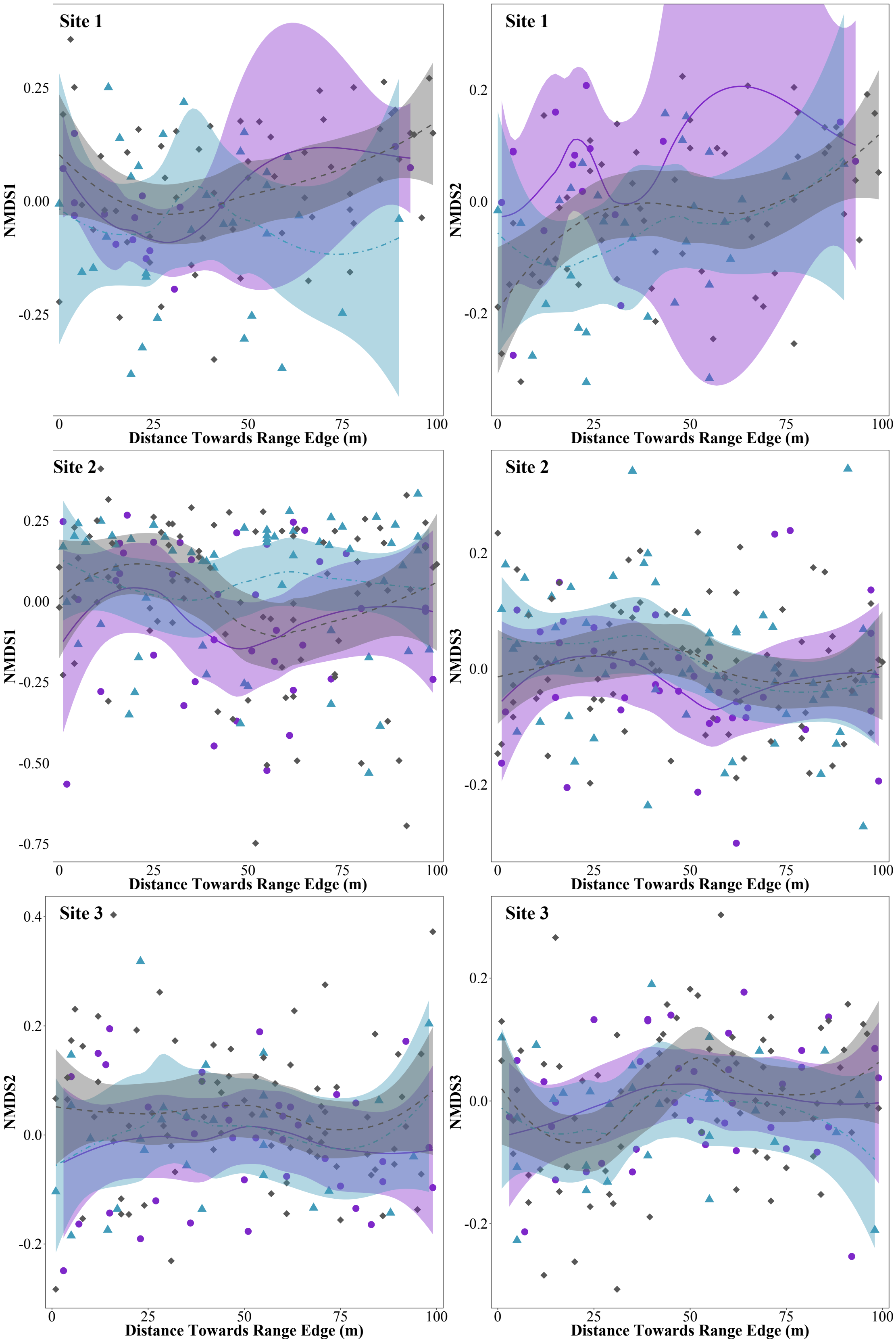


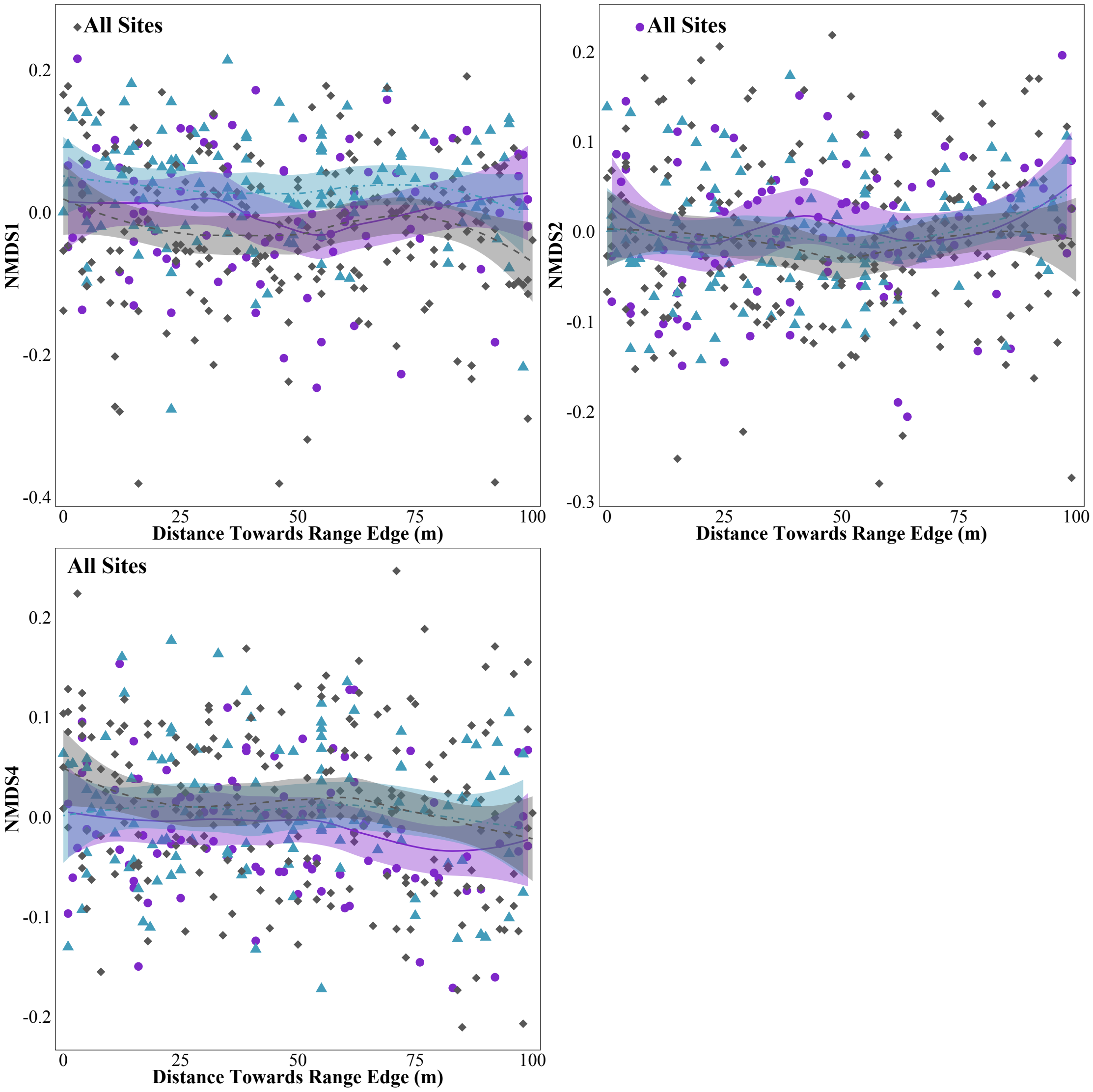
Supplementary Figure 3.1 Changing NMDS axes 1 and 2 scores along transects for treeless tundra (gray diamonds; dashed line) and emergents (orange circles; solid line) at Site Two. NMDS axis 1 is shown in text (Fig. 3.2). Each point indicates a seed plot with emergents present or a treeless tundra substrate. Distance towards range edge indicates position along the transect. Light shaded region represents 95% confidence intervals for microsite associations.


Site 1
NMDS1
0.2
0.0
-0.2
0
25
50
75
100
Distance Towards Range Edge (m)
Site 1
NMDS2
0.2
0.1
0.0
-0.1
-0.2
-0.3
0
25
50
75
100
Distance Towards Range Edge (m)
Site 2
NMDS2
0.9
0.6
0.3
0.0
-0.3
0
25
50
75
100
Distance Towards Range Edge (m)
Site 2
NMDS3
0.3
0.2
0.1
0.0
-0.1
-0.2
0
25
50
75
100
Distance Towards Range Edge (m)
Site 3
NMDS1
0.2
0.0
-0.2
0
25
50
75
100
Distance Towards Range Edge (m)
Site 3
NMDS3
0.2
0.0
-0.2
0
25
50
75
100
Distance Towards Range Edge (m)



Supplementary Figure 3.2 Changing NMDS scores along the treeline gradient for treeless tundra substrates (gray diamonds; dashed line) and seedlings (green circles; solid line) for all three sites separately and all sites combined. NMDS axis best showing divergence for each site shown in text (Fig 3.3). Each point indicates an individual or treeless tundra substrate. Distance towards range edge indicates position along the transect. Light shaded region represents 95% confidence intervals for microsite associations.


Site 1
NMDS1
0.25
0.00
-0.25
Distance Towards Range Edge (m)
0
25
50
75
100
Site 1
NMDS2
0.2
0.0
-0.2
Distance Towards Range Edge (m)
Site 2
NMDS1
0.25
0.00
-0.25
-0.50
-0.75
Distance Towards Range Edge (m)
Site 2
NMDS3
0.2
0.0
-0.2
Distance Towards Range Edge (m)
Site 3
NMDS2
0.4
0.2
0.0
-0.2
Distance Towards Range Edge (m)
Site 3
NMDS3
0.2
0.0
-0.2
Distance Towards Range Edge (m)



Supplementary Figure 3.3 Changes in NMDS scores along the treeline gradient for treeless tundra substrates (gray diamonds; dashed line) and adult groups (non-reproductive = purple circles; solid line, reproductive = blue triangles; dotdash line) for all three sites separately and all sites combined. NMDS axis best showing any divergence between groups shown in text (Fig. 3.4). Each point indicates an individual or treeless tundra substrate. Distance towards range edge indicates position along the transect. Light shaded region represents 95% confidence intervals for microsite associations.