

LANDSCAPE-SCALE ESTABLISHMENT AND POPULATION SPREAD OF YELLOW-CEDAR  
(*CALLITROPSIS NOOTKATENSIS*) AT A LEADING NORTHERN RANGE EDGE

By

John P. Krapek, BA

A Thesis Submitted in Partial Fulfillment of the Requirements

for the Degree of

Master of Science

in

Natural Resources Management

University of Alaska Fairbanks

December 2016

© 2016 John P. Krapek

APPROVED:

Dr. David L. Verbyla, Committee Co-Chair

Dr. Brian Buma, Committee Co-Chair

Dr. Paul E. Hennon, Committee Member

Dr. David V. D'Amore, Committee Member

Dr. Joshua A. Greenberg, Chair

*Department of Natural Resources Management*

Dr. David W. Valentine, Director of Academic Programs

*School of Natural Resources and Extension*

Dr. Michael Castellini, *Dean of the Graduate School*

## Abstract

Yellow-cedar is a long-lived conifer of the North Pacific Coastal Temperate Rainforest region that is thought to be undergoing a continued natural range expansion in southeast Alaska. Yellow-cedar is locally rare in northeastern portions of the Alexander Archipelago, and the fairly homogenous climate and forest conditions across the region suggest that yellow-cedar's rarity could be due to its local migrational history rather than constraints on its growth. Yellow-cedar trees in northern range edge locations appear to be healthy, with few dead trees; additionally, yellow-cedar tend to be younger than co-dominant mountain and western hemlock trees, indicating recent establishment in existing forests.

To explore yellow-cedar's migration in the region, and determine if the range is expanding into unoccupied habitat, I located 11 leading edge yellow-cedar populations near Juneau, Alaska. I used the geographic context of these populations to determine the topographic, climatic, and disturbance factors associated with range edge population establishment. I used those same landscape variables to model suitable habitat for the species at the range edge. Based on habitat modeling, yellow-cedar is currently only occupying 0.8 percent of its potential landscape niche in the Juneau study area. Tree ages indicate that populations are relatively young for the species, indicating recent migration, and that most populations established during the Little Ice Age climate period (1100 – 1850).

To determine if yellow-cedar is continuing to colonize unoccupied habitat in the region, I located 29 plots at the edges of yellow-cedar stands to measure regeneration and expansion into existing forest communities. Despite abundant suitable habitat, yellow-cedar stand expansion appears stagnant in recent decades. On average, seedlings only dispersed 4.65 m beyond stand boundaries and few seedlings reached mature heights both inside and outside of existing yellow-cedar stands. Mature, 100 – 200-year-old trees were often observed abruptly at stand boundaries, indicating that most stand boundaries have not moved in the past ~150 years. When observed, seedlings were most common in high light understory plant communities and moderately wet portions of the soil drainage gradient, consistent with the species' autecology in the region.

Despite an overall lack of regeneration via seed, yellow-cedar is reproducing via asexual layering in high densities across stands. Layering may be one strategy this species employs to slowly infill habitat and/or persist on the landscape until conditions are more favorable for sexual reproduction. This study leads to a picture of yellow-cedar migration as punctuated, and relatively slow, in southeast Alaska. Yellow-cedar's migration history and currently limited spread at the northeastern range edge should be

considered when planning for the conservation and management of this high value tree under future climate scenarios.

## Table of Contents

	Page
Title Page.....	i
Abstract .....	iii
Table of Contents.....	v
List of Figures .....	ix
List of Tables .....	xi
Acknowledgements .....	xiii
General Introduction .....	1
Chapter 1: Despite available habitat, migration of climate-threatened tree appears punctuated with last pulse during the Little Ice Age climate period.....	3
Abstract .....	3
Introduction .....	3
Objectives .....	5
Methods.....	6
Study Area Description .....	6
Yellow-Cedar Occurrence Mapping and Tree Ages .....	7
GIS Analysis.....	8
Null Landscape Sampling .....	10
Kernel Densities .....	10
Habitat Modeling .....	11
Vulnerability Analysis.....	11
Results .....	12
Yellow-Cedar Occurrence Mapping .....	12
Tree Ages .....	12
Kernel Densities .....	12
Habitat Modeling .....	13
Intersection Method .....	13
Logistic Regression.....	13
Vulnerability Analysis.....	14
Discussion .....	14
Yellow-Cedar Occurrence Mapping and Tree Ages .....	14

Yellow-Cedar Landscape Distribution .....	15
Habitat Modeling .....	17
Vulnerability Analysis.....	18
Conclusions .....	19
Figures .....	21
Tables.....	27
References .....	30
Chapter 2: Is a climate-threatened tree successfully expanding into suitable habitat at a leading northern range edge? .....	35
Abstract .....	35
Introduction .....	35
Objectives .....	38
Methods.....	38
Study Area Description .....	38
Plot Location at Stand Edges.....	39
Stand Development .....	40
Biotic Factors: Plant Community.....	41
Abiotic Factors: Snow and Soil Drainage.....	41
Statistical Analyses.....	42
Seedling Densities .....	42
Spatial Relationships among Seedlings and Trees.....	42
Results .....	44
Seedling Maturation and Spread .....	44
Stand Development .....	45
Spatial Relationships among Yellow-Cedar Seedlings and between Yellow-Cedar Seedlings and Overstory Trees .....	46
Seedling to Seedling.....	46
Seedling to Tree .....	46
Seedling Densities by Plant Community.....	46
Seedling Densities by Snow and Soil Drainage.....	47
Discussion .....	48
Seedling Maturation and Spread .....	48
Stand Development .....	49

Spatial Relationships among Yellow-Cedar Seedlings and between Yellow-Cedar Seedlings and Overstory Trees .....	50
Regeneration Densities by Plant Community.....	51
Regeneration Densities by Snow and Soil Drainage.....	51
Applicability to Other Systems .....	52
Conclusions .....	53
Figures .....	55
Tables.....	65
References .....	68
General Conclusions .....	73
General References.....	76



## List of Figures

Chapter 1	Page
Figure 1.1 Mapped yellow-cedar populations in study area near Juneau, Alaska.....	21
Figure 1.2 Estimated ages recorded for 10 yellow-cedar populations .....	22
Figure 1.3 Topographic, snow, and disturbance variables for yellow-cedar populations vs. null points..	23
Figure 1.4 Mean annual temperature for yellow-cedar populations vs. null points .....	24
Figure 1.5 Habitat modeling.....	25
Figure 1.6 Vulnerability analysis.....	26
Chapter 2	Page
Figure 2.1 Mapped yellow-cedar populations in study area near Juneau, Alaska.....	55
Figure 2.2 Stem map plot layout.....	56
Figure 2.3 Full stand stem map .....	57
Figure 2.4 Example test of spatial association .....	58
Figure 2.5 Full stand vs. interior subplot DBH distributions .....	59
Figure 2.6 Index of spatial association .....	60
Figure 2.7 Yellow-cedar regeneration densities in understory plant community associations .....	61
Figure 2.8 Regeneration densities across snow conditions.....	62
Figure 2.9 Regeneration densities across local hydrologic conditions .....	63
Figure 2.10 Photograph of a typical yellow-cedar stand boundary in the study area .....	64





## List of Tables

Chapter 1	Page
Table 1.1 GIS data layers and source. ....	27
Table 1.2 Yellow-cedar occurrence summary statistics. ....	28
Chapter 2	Page
Table 2.1 Information recorded for stem-mapped trees and yellow-cedar seedlings .....	65
Table 2.2 Mean regeneration densities per hectare by subplot type .....	66
Table 2.3 Count of positive, negative, and non-significant (random) spatial associations tested. ....	67



## Acknowledgements

I would like to sincerely thank my advisers, Dr. Brian Buma and Dr. David Verbyla, for their generous advice, guidance, and wisdom throughout my studies. Brian Buma taught me how to look at landscapes, think analytically, and write like an ecologist. Dave Verbyla helped me hone invaluable GIS skills, and taught me the importance of developing concise research questions and analyses. Thanks so much to both Dave and Brian for taking me on as a non-traditional student based in Juneau, and for helping me make it work.

Thank you to my two committee members, Dr. David D'Amore and Dr. Paul Hennon, for their huge energy and support, and making me feel like my project was already a success from day one. Dave D'Amore always has a solution to make things happen, and taught me to see beyond the plant community. Paul Hennon has unmatched wisdom and humor, and always emphasized the importance of the bigger, range-wide picture. Thanks to my whole committee for taking me along on their other projects, and for helping me become a well-rounded ecologist. I use the word "we" throughout my manuscripts because each is a collaborative effort with my graduate committee.

My project would not have been possible without my outstanding field assistants, Alex Botelho, William Bottorf, and Danny Cooper, who put up with lots of long marches, scrambling down cliffs to map wayward yellow-cedar trees, and strained eyeballs from looking through the laser rangefinder all day. Thank you to Lauren Hopson for starting the work of locating Juneau's yellow-cedar stands back in 2008.

Thank you to the Bonanza Creek Long Term Ecological Research (LTER) program, Alaska Experimental Program to Stimulate Competitive Research (EPSCoR), UAF Center for Global Change, and the Alaska Coastal Rainforest Center (ACRC) for funding support. Members of the USFS Juneau Forestry Sciences Lab staff provided generous support and guidance for my project. Thank you to the UAF School of Natural Resources and Extension (SNRE) faculty and staff for supporting my project and helping me develop as an ecologist

I would like to acknowledge Jon R. Martin, and his fellow authors of the "Forest Plant Association Management Guide – Chatham Area, Tongass National Forest", for putting together a seminal work on the vegetation ecology of the northern Tongass which was a critical reference for my yellow-cedar studies. I think early publications like this are forgotten at times, but have many of the answers we are seeking.

Most of all, thank you to my friends and family for endless support. Thanks to Sonia Ibarra and Danny Green, my cedar friends. Thanks to my parents, and KJ and Meredith Krapek, for all your encouragement. Thanks to Lucy the dog for making field work more fun, if less efficient. Thanks to

Maggie Chan for always making me laugh, being there for me, and going into the field with me when no one else would.

## General Introduction

“I think the cedar are just down there, where the slope flattens out...what do you think, John, can you smell them yet?” Dr. Dave D’Amore shouts back as we crash down the hill through blueberry and menziesia shrub thickets, grabbing branches as we go to keep our feet from slipping out from under us on the wet vegetation beneath. Having just climbed 150 meters up the ridge from Bridget Cove near Juneau, Alaska, we are descending down the other side, on the hunt for yellow-cedar (*Callitropsis nootkatensis*) trees which are rare in these forests. I am exhausted from the steep ascent and wet on both sides of my rain gear – damp with sweat inside from keeping up with Dave, and covered in water on the outside from the ever-wet vegetation of the southeast Alaskan rainforest through which we are trudging. But now we are close to finding one of the hidden yellow-cedar groves, where we can begin to investigate when these trees got here, and how they might be expanding into Juneau’s forests.

When we hit the toe slope, the shrub thickets open up and the walking changes. We’re no longer fighting our way through tangled shrubs, but now trying to step over prehistoric, shiny green skunk cabbage leaves which are as wide and long as palm fronds. Dr. Brian Buma, my mentor, is also along, and I can sense we are all trying to be the first one to spot a yellow-cedar. “Classic forested wetland,” Dave reports, as I squint at the silvery bark of a tree in the distance, trying to determine if it is what we are looking for before I call it out prematurely. “It’s a cedar!” Brian yells, a few steps ahead of us, as the long strips of fibrous bark and the scraggly, yet elegant, droops of foliage comes into view. We’ve found it! Whoever thought it could be so fun to find trees in the forest? This would be one of 11 small yellow-cedar populations scattered around the Juneau road system that we would eventually find and map, and for better or worse, I am now always on the lookout for yellow-cedar when I’m in the woods.

We are studying these unique and locally prized trees for a few reasons. First, nobody is sure why yellow-cedar are so rare near Juneau, but leading hypotheses suggest that yellow-cedar may be undergoing a continued natural range expansion in the Gulf of Alaska region following the retreat of ice from the Last Glacial Maximum (Cararra et al. 2007, Hennon et al. 2012, Buma et al. 2014). We wanted to know if ages of these 11 populations, and their proportional occupancy of suitable habitat for the species at this northeast range edge, supported these hypotheses and suggest ongoing migration. Or, are other factors responsible for constraining yellow-cedar’s range near Juneau? Second, we wanted to determine if yellow-cedar are expanding into local forests, and if so, what types of communities they are invading and how successfully. Is the yellow-cedar range actively expanding near Juneau?

Understanding the ability of plant species to expand their ranges in an era of unprecedented global

change is a leading research and conservation concern (Davis and Shaw 2001, Malcolm et al. 2002, Loarie et al. 2009, Hille Ris Lambers et al. 2015).

Against the backdrop of these questions, yellow-cedar trees have experienced widespread mortality in southeast Alaska and adjacent British Columbia in the last century (Hennon et al. 2016, Buma et al. 2016). A long-term, systematic research program has tied yellow-cedar mortality, termed yellow-cedar decline (YCD), to climatic changes in the region since the end of the Little Ice Age in approximately 1850 (Hennon et al. 2012, Wiles et al. 2014). Diminishing winter snowpacks, which are critical for protecting yellow-cedar's shallow fine roots from periodically freezing air temperatures, are the primary predisposing cause of yellow-cedar mortality in the region (Schaberg et al. 2011, Hennon et al. 2012). Yellow-cedar decline has been observed only ca. 100 km to the south of Juneau (Dubois and Burr 2015). With future human-accelerated climate warming projected to further diminish snowpacks in the region, YCD is expected to emerge farther north in the yellow-cedar range (Hennon et al. 2016) and potentially threaten some Juneau populations.

The context of YCD makes studying yellow-cedar's migration and expansion at a northern range edge all the more critical. Is yellow-cedar likely to continue its expansion north and east to potentially snowier and more favorable conditions, or does yellow-cedar not possess the dispersal/adaptive capacity to keep its leading edge ahead of the trailing edge of YCD? This study explores yellow-cedar migration and expansion at this leading northeast range edge for the species in an attempt to shed light on some of these questions.

The two studies presented here offer an integrated approach to yellow-cedar migration at two separate scales. In Chapter 1, we investigate yellow-cedar establishment around the Juneau range edge at the broader landscape scale, and ask: when did trees arrive near Juneau, and how much suitable habitat in the study area do they currently occupy? In Chapter 2, we focus in on stand edges to explore yellow-cedar expansion into existing forests. How do yellow-cedar seedlings interact with existing plant communities at stand edges, and what landscape factors are correlated with yellow-cedar seedling success? This thesis is an initial small step, of hopefully many, to understanding a piece of yellow-cedar's recent migration history and future dispersal capacity in southeast Alaska.

## Chapter 1: Despite available habitat, migration of climate-threatened tree appears punctuated with last pulse during the Little Ice Age climate period<sup>1</sup>

### Abstract

When a species' range lags behind current climate conditions, and therefore only occupies a portion of its fundamental niche on the landscape, projecting future range shifts based on climate alone can be challenging. Factors leading to migration lags behind climate, such as a species' limited dispersal capacity near a range edge, can compound the difficulty of the future range projections and are important to consider. Yellow-cedar, a slow-growing, long-lived conifer of the North Pacific Coastal Temperate Rainforest region is hypothesized to be undergoing a continued natural range expansion in the northern Alexander Archipelago of southeast Alaska. We located 11 leading range edge yellow-cedar populations near Juneau, Alaska, determined their proportional occupancy of modeled potential habitat at the range edge, and estimated approximate population ages. Despite abundant potential habitat, and having existed in the study area > 675 years, yellow-cedar has only occupied a small proportion (< 0.8 percent) of suitable habitat. Yellow-cedar appears to have undergone a past pulse of successful regeneration during the Little Ice Age climate period when it first established in the study area, with little apparent stand expansion in recent decades. Yellow-cedar's episodic, relatively slow migration may have implications for conservation planning, especially as the species trailing edge is approaching the leading edge in the region.

### Introduction

The current pace of climate change and its influence on potential ecosystem distributions (Loarie et al. 2009) necessitates an examination of species' spread at their leading range edges and contraction at trailing edges. Numerous studies have shown that plant species are already moving poleward and uphill at rapid rates (Parmesan and Yohe 2003), but there are concerns that rates of migration might not keep pace with changing climate (Davis and Shaw 2001, Malcolm et al. 2002, Loarie et al. 2009, Hille Ris Lambers et al. 2015). For species potentially not keeping pace with climate, assessing range dynamics at leading and trailing edges, *as well as* migration history, will be essential for the most accurate inferences of realized niches in future climate scenarios (Feurdean et al. 2013, Hille Ris Lambers et al. 2015). An

---

<sup>1</sup> Krapek, J., Hennon, P.E., D'Amore, D.V., & Buma, B. Despite available habitat, migration of climate-threatened tree appears punctuated with last pulse during the Little Ice Age climate period. Prepared for submission in the Journal of Biogeography.



understanding of non-equilibrium population dynamics and lagged responses to climate is essential for evaluating the validity of implicit assumptions in biogeographical models that try to predict population distributions under future climate scenarios (Johnstone and Chapin 2003).

The paleobotanical record serves as a strong foundation for understanding plant species' movements in periods of past climatic change, and is replete with examples of rapid tree migration in response to abrupt climate shifts (Petee 2000, Pearson and Dawson 2005, Ordonez and Williams 2013). However, the fossil pollen record can be a blunt tool which may miss the presence of small, low density populations (McLachlan et al. 2005, Pearson 2006) or overestimate the presence of local taxa (Petee 1986). Studying modern tree migrations in real time, on the other hand, offers a shorter snapshot of response to climate, but may ultimately allow for more accurate inferences, especially when a species lags behind current climate equilibrium dynamics (Johnstone and Chapin 2003).

Yellow-cedar (*Callitropsis nootkatensis*) is a conifer of the North Pacific Coastal Temperate Rainforest (NPCTR) region that is hypothesized to be undergoing a continued natural range expansion, filling in areas that were exposed as the Laurentide Ice Sheet retreated from the Last Glacial Maximum (LGM) ca. 20,000 years before present (Carrara et al. 2007, Hennon et al. 2012, Buma et al. 2014). Yellow-cedar is noted to be absent in certain portions of the landscape in southeast Alaska despite what appears to be suitable habitat (Martin et al. 1995). Except for the presence of yellow-cedar, community composition, climate, soils, and geomorphology are otherwise similar between yellow-cedar and many non-yellow-cedar forests (e.g., *Tsuga*-dominated communities) in the region (Martin et al. 1995, Hennon et al. 2016), suggesting that competition is not precluding yellow-cedar from establishing where it is not already present. Additionally, yellow-cedar planting experiments have successfully occupied habitat outside of its contiguous range in the region (Hennon et al. 2016).

Yellow-cedar's relatively slow migration following deglaciation, and subsequent patchy distribution, may be due to a combination of factors including its low reproductive capacity, apparently limited seed dispersal distance compared to sympatric conifers, and strict germination requirements (Hennon et al. 2016). Although tree pollen became present in the regional paleoecological record ca. 13,000 years before present (Hansen and Engstrom 1996), and climate transitioned to a regime similar to today ca. 4,500 years before present (Heusser et al. 1985, Mann 1986), yellow-cedar pollen only became abundant in southeast Alaska ca. 2,200 years before present (Ager et al. 2010). However, yellow-cedar's postglacial history in the region is poorly understood overall, partly because it was ignored in early pollen studies (Heusser 1960) due to the fragility and lack of decay resistance of its pollen, as well as the difficulty in identifying its pollen compared to other members of the Cupressaceae (Hennon et al. 2016).

Because of the dearth of regional pollen studies including yellow-cedar, examining yellow-cedar distribution shifts through estimating range edge population ages, documenting expansion of advanced stands, and modeling suitable habitat vs. current occupancy of that habitat is an alternative way to examine a lingering ecological question.

In addition to its apparent dis-equilibrium with climate at its northern range edge, yellow-cedar forests in southeast Alaska and British Columbia (ca. 100 km southwest of the current northeast range edge) are experiencing widespread mortality (~400,000 ha; Buma, Hennon, et al. 2016), known as yellow-cedar decline (YCD), related to the rapid climate changes in the region since the end of the Little Ice Age, ca. 150 years before present (Hennon et al. 2012). Mortality attributed to this phenomena is occurring only ~100km south of the current northeastern range edge documented in our study (Dubois and Burr 2015). Diminishing winter snowpacks, which are critical for protecting yellow-cedar's shallow fine roots from freezing air temperatures, are the primary predisposing cause of yellow-cedar mortality in the region (Schaberg et al. 2011, Hennon et al. 2012). Mean winter temperatures in Southeast Alaska have historically been close to freezing; as snowpacks are further diminished with small winter temperature increases, new portions of the yellow-cedar range will become vulnerable to sporadic winter freezing events (Hennon et al. 2016, Buma, Hennon, et al. 2016).

With anticipated future climate changes in the NPCTR region and potential emergence of YCD farther north in its range, assessing if yellow-cedar is continuing its post-glacial migration, and the pace of that migration, will be essential for understanding the species' adaptive capacity under future climate scenarios. As yellow-cedar's trailing edge approaches its leading edge in southeast Alaska, determining if the species has the natural migration capacity to keep pace with shifting climate is a critical research and conservation question; the U.S. Forest Service (USFS) climate adaptation strategy for yellow-cedar in Alaska (Hennon et al. 2016) identified assessing the postglacial colonization of yellow-cedar as a leading research priority.

### *Objectives*

Our objective in this study was to locate advanced, leading edge yellow-cedar populations near Juneau, Alaska, which lie beyond the contiguous northeast edge of yellow-cedar's current range, and answer the following questions:

1. When did advanced yellow-cedar populations establish, and is that establishment continuing today?

2. Does additional suitable habitat currently exist on the landscape for continued yellow-cedar expansion? Or, has yellow-cedar filled its potential niche in the area?
3. Will leading edge populations become vulnerable to YCD in future climate scenarios?

To answer these questions, we mapped the geographic extent of 11 advanced yellow-cedar populations and estimated their ages. We compared topographic, snow cover, and disturbance exposure metrics for mapped yellow-cedar stands with areas on the landscape that are not currently occupied by yellow-cedar forests to determine if there were spatio-topographic trends for yellow-cedar establishment. Estimated population ages were compared to each other, and to a past climate reconstruction from the region, to understand timing of yellow-cedar establishment in the study area.

Additionally, we modeled potential yellow-cedar habitat in two ways. First, suitable habitat was modeled as areas on the landscape that host the same range of values for topographic, climate, and disturbance variables as where yellow-cedar stands occur, and second, via logistic regression to determine the likelihood of yellow-cedar habitat on the landscape based on the current landscape features supporting leading-edge populations. Finally, we compared locations of yellow-cedar populations to winter snow conditions under two future climate models to determine if these currently healthy yellow-cedar populations may become vulnerable to future decline.

## Methods

### *Study Area Description*

The study area was located near Juneau, Alaska, USA, which lies beyond yellow-cedar's current contiguous northeast range edge (Figure 1.1). Yellow-cedar is rare in the surrounding forests, with apparently large expanses of unoccupied, but suitable habitat in the region (Martin et al. 1995).

Juneau's climate is cool maritime despite its high latitude (58°N), caused by the moderating influence of the Alaska current in the Pacific Ocean (Martin et al. 1995). Mean monthly temperatures range from -2 to 14°C at sea level throughout the year (NOAA 2016), and strong topographic gradients cause significant variability at fine scales. Precipitation is high, ranging from 1,400 to 2,300 mm annually with no summer drought period, leading to a landscape relatively free from large disturbances (e.g., fire, large insect outbreaks) and a mosaic of late seral forests, peatlands, and shrublands as the dominant vegetative communities (Martin et al. 1995). The predominant forest disturbance in the region is localized windthrow of trees of generally <1000 m<sup>2</sup> patches (Ott and Juday 2002, Buma and Barrett 2015), varying in frequency and intensity by landscape position (Nowacki and Kramer 1998, Ott and

Juday 2002), with occasional stand-replacing blowdown events or localized landslides related to wind and precipitation (Buma and Johnson 2015).

Snowpack in the region is highly variable, ranging from 1,000 mm in snow-water equivalent (SWE) annually at sea level to 5,000 mm on mountain peaks, on average. Year to year variability in snow accumulation is also high, and during mild winters low elevation areas may remain snow-free for much of the winter (Martin et al. 1995). Because mean winter temperatures are close to 0°C at sea level, future climate warming is predicted to result in drastically reduced precipitation as snow (PAS) and has profound impacts for ecosystem functioning in the region (Shanley et al. 2015).

Tree diversity is low, with western hemlock (*Tsuga heterophylla*) dominating most of the moderate to well-drained, stable sites; mountain hemlock (*T. mertensiana*) replaces western hemlock in the subalpine zone (Martin et al. 1995). Sitka spruce (*Picea sitchensis*) dominates in frequently disturbed areas (e.g., floodplains), where its rapid growth is favored. Broadleaved species are primarily limited to alder (*Alnus* spp.) and black cottonwood (*Populus trichocarpa*) in areas of disturbance. Yellow-cedar and mountain and western hemlocks can co-dominate on stable, moderately to marginally productive sites with poor drainage and/or shallow soils. Because yellow-cedar is relatively shade intolerant compared to western hemlock (Harris et al. 1974), it is more competitive in sites with open canopies, and can become co-dominant where light conditions (e.g., canopy gaps) allow for successful reproduction (Martin et al. 1995).

#### *Yellow-Cedar Occurrence Mapping and Tree Ages*

Eleven yellow-cedar populations, defined by greater than 250 m separation between mature trees, were identified in the study area via a combination of previous USFS mapping, community knowledge, and a targeted helicopter survey. While visiting each of the populations on the ground, we identified patches of mature yellow-cedar trees (>1.4 m tall) within the population, as well as individual lone trees at population edges. When we located a patch of mature yellow-cedar trees, we circumnavigated its edge, recording GPS coordinates approximately every 10 m along the boundary. If a tree or patch of trees was located less than 30 m from the patch being actively mapped, the boundary was extended to include those trees. We used 30 m as a limit for considering a lone tree or patch as a separate yellow-cedar occurrence, because mature yellow-cedar trees are approximately 30 m in height on average (Burns and Honkala 1990) and there is currently a lack of information on average seed dispersal distances for mature trees (Hennon et al. 2016); therefore, we assumed 30 m is a reasonable estimate of the average maximum dispersal distance for a mature tree, and that trees beyond that distance may

be from a separate establishment event. Within the broader 11 populations we visited, patches of multiple trees (n=27) and individual lone trees (n=14) were considered independent events of yellow-cedar establishment on the landscape, and were used for all topographic analyses described below. Patches and lone trees (total n=41) are collectively referred to as “occurrence” in all following sections. The 11 broader populations were compared for establishment age only.

At each population, increment cores were taken for the largest trees to determine an approximate age for the population. Cores were taken from 10 of 11 populations; no cores were taken at the 11<sup>th</sup> population due to equipment failure. Trees were cored approximately 1 m above the ground, and aged using standard methods (Stokes and Smiley 1968). Because populations range in size from a single tree (smallest) to over 150 ha (largest), we sampled proportionally more trees in smaller populations than larger population (n=1 to n= 18). In total, 96 separate yellow-cedar trees were cored. Corrections were not applied to tree cores for height from base of tree, or rings missed due to internal decay. Additionally, we targeted only large trees; large trees are often older, but not necessarily the oldest trees in each population, as microsite and hydrology control size-growth patterns in the region (Buma, Krapek, & Edwards 2016). Therefore tree ages reported here are minimum ages and potentially underestimate actual population ages.

### *GIS Analysis*

We examined ten landscape variables (five topographic, three related to snow cover, one disturbance metric (wind exposure), and mean annual temperature; Table 1.1) to compare the landscape features where yellow-cedar occurs to locations where yellow-cedar is not known to be present. These variables were chosen because topography, specifically elevation and soil drainage, is a strong control on forest productivity and plant community composition in the region (Alaback 1982, Buma, Krapek, & Edwards 2016, Caouette et al. 2016). Lack of snow cover is the leading risk factor for yellow-cedar decline, and snow may additionally aid yellow-cedar establishment by providing protection for yellow-cedar seedlings from winter browse by Sitka black tailed deer (*Odocoileus hemionus sitchensis*; Hennon et al. 2016) and moose (*Alces alces*; personal observation).

Because yellow-cedar is a slow-growing tree that is more competitive in high light conditions in the region (Martin et al. 1995), it may be dependent on disturbance to establish and/or persist in old-growth forest conditions with low canopy turnover. Therefore, we examined a wind exposure index (Buma and Barrett 2015) to determine if yellow-cedar established in more wind-prone areas, which have a higher incidence of gap-phase and stand-replacing blowdown events (Nowacki and Kramer 1998).

For topographically derived variables, we utilized an interferometric synthetic aperture radar (IfSAR) bare-earth digital elevation model (DEM) created by the U.S. Geological Survey (USGS 2015). Using this dataset, we derived aspect, compound topographic index, elevation, slope, and solar radiation all at 5 m resolution. Compound topographic index (CTI), a measure of water accumulation across the landscape, was computed as:

$$CTI = \ln\left(\frac{a}{\tan(b)}\right) \quad \text{Equation 1.1}$$

where “a” is the upslope contributing area, and “b” is the slope in radians (Gessler et al. 1995).

For snow variables, we used the National Park Service (NPS) and Geographic Information Network of Alaska (GINA) snow cover metrics for Alaska derived from the MODIS daily snow cover product (Lindsay et al. 2015). Data for the 2001 – 2014 snow seasons were downloaded at 500 m resolution, and resampled using bilinear interpolation to match the 5 m resolution of IfSAR data layers. Bilinear interpolation was chosen because snow cover generally varies smoothly as a function of topography at this scale. Because yellow-cedar roots are dependent upon a persistent insulating snowpack for protection from winter and spring freezing events (Schaberg et al. 2011, Hennon et al. 2012), we used continuous snow season (CSS) metrics from Lindsay et al. (2015). Continuous snow season data represent 14 day or more snow cover periods, rather than snow on/off at short intervals within pixels. Persistent snowpacks (14 days or longer) are more likely to provide protection to roots during freezing periods than sporadic snow coverage (Schaberg et al. 2011).

We used three CSS metrics: duration (length of the longest CSS segment), last day of snow, and total days in the continuous snow season (i.e., number of days in all CSS segments for each pixel). Duration and total snow season days relate to the total winter snow protection from freezing events, while last day of snow coverage is known to be important for protection of yellow-cedar roots from late spring freeze events (Schaberg et al. 2011). Means and minimums were computed for the entire period of snow data (2001 – 2014) available. Means represent normal snow conditions for the available satellite record, while minimums are indicative of the minimum snow requirements for yellow-cedar occurrence in the study area.

To examine the potential role of disturbance in creating or precluding establishment opportunities, we used a relative wind exposure index (Buma and Barrett 2015). The index represents topographic sheltering to regional storm tracks (southeast, south). We resampled the layer using bilinear interpolation to match the 5 m resolution of other data layers.

Elevation is an important control on species distribution, seedling initiation, and climate in the region (Harris et al. 1974, Caouette et al. 2016), with aspect being relatively unimportant for forest

productivity (Buma, Krapek, & Edwards 2016). Therefore, we used elevation as a proxy for most climate variables in analyses throughout the paper. For an additional test of the influence of climate on yellow-cedar establishment, we examined mean annual temperature throughout the study area. Mean annual temperature data from the WorldClim dataset (Hijmans et al. 2005) are available at a 30-arc-second resolution and were resampled using bilinear interpolation to match the 5 m resolution of topographically-related data layers.

Mean values of each landscape variable were calculated for each yellow-cedar occurrence (n=41) on the landscape.

#### *Null Landscape Sampling*

We randomly sampled the landscape where yellow-cedar is absent (“null points”) to compare areas of establishment to areas of presumed absence using the following criteria. We first used the 2011 National Land Cover Database (Homer et al. 2015) to remove non-vegetated pixels, including perennial ice/snow, open water, barren land, and all developed categories. Next, we removed all areas above 593 m in elevation, which is the highest elevation at which yellow-cedar was located. Well-developed, closed canopy forests occur up to approximately 600 m in the region (Ott and Juday 2002), with patchier forests occurring to approximately 850 m (Buma, Krapek, & Edwards 2016). Jovan (2011) identified the mean elevational occurrence of yellow-cedar in Alaska as 297 m, and in an analysis of Forest Inventory and Analysis plots in the northern Alaskan panhandle, Caouette et al. (2016) show that above 600 m, yellow-cedar presence decreases to below 20 percent. Therefore, limiting our null points to 593 m is a conservative approach to examine the elevational range of where we know yellow-cedar to occur in the local study area.

Finally, we removed mapped yellow-cedar occurrences from the null landscape. We randomly sampled all topographic variables 1,000 times (null points) for comparison to values where yellow-cedar are present.

#### *Kernel Densities*

Kernel density plots were constructed for each topographic variable using R software (R Development Core Team 2015) to compare the distribution of values for yellow-cedar occurrences (n=41) to random null points (n=1,000). Kruskal-Wallis rank sum tests were performed to determine if

distributions were significantly different ( $\alpha = 0.05$ ). A Holm-Bonferroni correction was applied to the 13 Kruskal-Wallis rank sum tests performed to correct for the family-wise error rate.

### *Habitat Modeling*

Because little work has been done on modeling potential habitat for species not currently at climatic equilibrium (Veloz et al. 2012), we used two complimentary approaches to estimate potential yellow-cedar habitat in the study area. First, we computed the full range of values for each topographic, snow cover, and disturbance variable in which yellow-cedar occurred. We then identified any area on the landscape that fell within the full range of those variables (i.e., the intersection of current conditions where yellow-cedar is known to occur in the study area). This approach does not take into account biotic factors such as competition or seed dispersal, but has the advantage of identifying habitat that meets the same topographic and environmental characteristics of areas where yellow-cedar already does grow.

Second, we used a binomial generalized logistic regression (GLM, logit link) model to identify likely yellow-cedar habitat based on the current topographic values at the geographic mean center of yellow-cedar occurrences. This approach is useful for identifying highly likely yellow-cedar habitat based on where yellow-cedar is currently growing, but does not take into account the fact that yellow-cedar may not be fulfilling its potential niche within the study area and is much more restrictive than the first intersection method. Together, the two methods are intended to approximately bracket the range of potential habitat on the landscape.

### *Vulnerability Analysis*

To estimate vulnerability to future climate in relation to yellow-cedar decline, we used climate projections for the mean winter temperature (defined as the coldest quarter of the year; Hijmans et al. 2005) as a proxy for future winter snow coverage in the study area. A low (RCP 2.6) and high (RCP 8.5) emissions scenario from the HadGEM2-ES coupled Earth System Model (Collins et al. 2011) were examined for the study area in two bidecadal periods centered around 2050 and 2070. We classified the study area as having mean temperature in the coldest quarter either above or below 0°C as a proxy for future low snow vs. historically normal snow conditions, respectively. This threshold is ecologically meaningful for yellow-cedar mortality (Hennon et al. 2012) and has been shown to be useful in regional yellow-cedar decline mapping (Buma, Hennon, et al. 2016). Mapped yellow-cedar populations were



overlaid with future coldest quarter climate scenarios data to determine which areas might be susceptible to low snow coverage in the future.

## Results

### *Yellow-Cedar Occurrence Mapping*

Within the 11 yellow-cedar populations we visited, 41 distinct yellow-cedar occurrences were mapped, including 14 lone individuals, and 27 patches ranging in size from <0.01 ha to a 151 ha, totaling 286 ha. Yellow-cedar occurrences are shown in Figure 1.1. Summary statistics for all yellow-cedar occurrences are included in Table 1.2.

### *Tree Ages*

The oldest yellow-cedar tree in the study area had a minimum age of 675 years, though with substantial heart rot this is an underestimate of its true age. The youngest population had a minimum age of 89 years and was only 0.04 ha in size. The mean age of the 10 populations measured in the study area was 295 years (median = 232). Eight out of ten populations measured for age appear to have established during the Little Ice Age climate period of approximately 1100-1850 AD (Wiles et al. 2014; Figure 1.2).

### *Kernel Densities*

Yellow-cedar occurrences were not randomly distributed for several topographic characteristics (Figure 1.3). Yellow-cedar occurrences tended strongly towards north-facing slopes ( $p = 0.03$ ) compared to random null points; the null points were distributed fairly evenly across all aspects. Solar radiation ( $p = 0.04$ ) and wind exposure index ( $p = 0.04$ ) were also significantly different for yellow-cedar occurrences, related to yellow-cedar's prevalence on north-facing slopes which receive less solar radiation and are more sheltered from prevailing south, southeast storm winds (Buma and Barrett 2015).

None of the three snow variables examined was significantly different between the yellow-cedar occurrences and null points. Mean annual temperature showed no significant difference between the occurrence of yellow-cedar and random null points (Figure 1.4). Elevation similarly showed no significant difference between yellow-cedar occurrences and null points, nor did slope ( $p > 0.05$ ). Although there was no significant difference in CTI between presence and absence points, yellow-cedar

showed a high density at CTI values of approximately 5.0, which represent areas of the landscape with moderate water accumulation.

### *Habitat Modeling*

#### Intersection Method

The modeling approach in which we identified areas of the landscape that fell within the same range of values of each landscape variable as the yellow-cedar occurrences (i.e., fell within the same range of slope values, and also aspect values, and also snow cover values, etc.) suggests a substantial amount of suitable potential yellow-cedar habitat in the study area (Figure 1.5a). Areas not considered suitable habitat using this methodology include only very low elevation areas (no yellow-cedar occurred < 28 m), and pixels at the extremes of snow cover variables, compound topographic index, slope, and solar radiation. Despite their tendency towards north-facing slopes, yellow-cedar occurred across all aspects and wind exposure index values, and therefore, these variables were not useful for excluding potential habitat using this method.

The null landscape area we identified as capable of supporting forests, but  $\leq 593$  m (the highest elevation we observed yellow-cedar), is 48,456 ha in size. Within the null landscape, there are approximately 37,797 ha of potential yellow-cedar habitat based on the range of landscape values where yellow-cedar currently grows.

#### Logistic Regression

The GLM model highlighted snowy, north-facing slopes with moderate CTI values throughout the study area as having a high likelihood of suitable yellow-cedar habitat (Figure 1.5b). Yellow-cedar has only established in a small portion of these locations, however. Steeply sloped areas, and locations with a high CTI (extremely wet) are highlighted as having a very low likelihood of yellow-cedar occurrence.

Yellow-cedar is currently growing in areas identified by the GLM model as having a 0.01 probability of occurrence. Therefore, if 0.01 probability of occurrence is used as a threshold for yellow-cedar habitat, this method identifies 40,110 ha of potential habitat within the 48,456 ha null landscape. The median GLM value where yellow-cedar currently occurs is 0.08. If we exclude all areas below 0.08 as low likelihood of yellow-cedar habitat, then there are approximately 6,731 ha of high likelihood habitat within the study area.

### *Vulnerability Analysis*

Yellow-cedar populations in the study area may become vulnerable to conditions known to lead to yellow-cedar decline only under the high emissions (RCP 8.5) scenario examined (Figure 1.6). In the bidecadal period centered around 2050, only low elevation stands (<165 m) would be potentially vulnerable to decline. In 2070, additional mid-elevation (<400 m) stands may become vulnerable; only the three highest elevation populations (> 400 m) would hypothetically remain safe from risks due to low snow accumulation. In the RCP 2.6 low emissions scenario, all portions of the study area currently supporting yellow-cedar populations maintain a mean winter temperature below 0°C, indicating that they would likely maintain a winter snowpack through much of the period when yellow-cedar roots need protection from freezing events.

### Discussion

#### *Yellow-Cedar Occurrence Mapping and Tree Ages*

Our mapping effort confirms that there are substantial areas of unoccupied potential habitat along yellow-cedar's sparsely distributed northeastern range edge. Tree ages indicate that populations are relatively young (median age 232 years) compared to the average (500 – 750 years; Hennon et al. 2016) and maximum (>1,000 year; Burns and Honkala 1990) ages reported for mature trees of the species. Eight out of ten populations established during the Little Ice Age, a period cooler and snowier than today (Wiles et al. 2014). This finding is consistent with observations by Hennon et al. (1990) and Beier et al. (2008) which show that most living, mature yellow-cedar trees in their plots throughout southeast Alaska regenerated and grew to canopy status during the Little Ice Age.

Previous work (Hennon et al. 2012) has hypothesized that yellow-cedar is undergoing a continued natural migration from glacial refugia on the outer coasts of southeast Alaska and British Columbia that were ice free during the LGM (Carrara et al. 2007). Shore pine (*Pinus contorta* ssp. *contorta*) appears to have rapidly recolonized the landscape from nearby glacial refugia following the LGM (Peteet 1991) where yellow-cedar may have also been present (Hennon et al. 2012), or may have made a rapid migration from south of the ice sheet immediately following deglaciation. Western hemlock and Sitka spruce, the two most abundant conifers in the region today, appear to have made a rapid migration from south of the ice sheet to fill in much of the temperate rainforests of southeast Alaska shortly after initial shore pine dominance (Heusser 1960, Peteet 1986, Hansen and Engstrom 1996, Ager et al. 2010). Future paleobotanical studies that focus on distinguishing yellow-cedar pollen from other species could fill in the existing knowledge gap on the rates of Holocene yellow-cedar migration.

Yellow-cedar's present-day dispersal limitations, including its low reproductive capacity, limited seed dispersal, slow growth, and shade intolerance compared to western hemlock and Sitka spruce (Hennon et al. 2016) may be responsible for its currently limited infilling of habitat in the region. However, the population ages we report here (median age 232 years), and stands of healthy co- and sub-dominant yellow-cedar trees which appear to have invaded existing hemlock-spruce forests, indicate that past climate or forest conditions may have favored a pulse of yellow-cedar regeneration during the Little Ice Age. Yellow-cedar's longevity, tolerance of stress conditions, and high relative survivorship compared to sympatric forest trees (Lertzman 1995, Hille Ris Lambers et al. 2015) may allow it to persist on the landscape until conditions are favorable for colonization and regeneration, ultimately leading to a punctuated and relatively slow migration. Preliminary molecular DNA work from yellow-cedar foliage collections across its range suggest that Alaska populations were founded by diverse sources and expanded at an exponential rate at some point in the past, perhaps during the Little Ice Age (Cronn et al. 2014, Hennon et al. 2016).

Yellow-cedar has taken >675 years to occupy 286 ha of the 37,797 ha, or < 0.8 percent, of potentially available habitat capable of supporting yellow-cedar forests within the study area (ignoring factors such as dispersal, soil type, and biotic competition). With a return to cooler and snowier conditions at some point in the future, yellow-cedar could go through another pulse of successful regeneration to fill in available habitat; however this currently appears unlikely given projected future climate scenarios (Hennon et al. 2016). More detailed age structure work at these range edge stands, in addition to paleobotanical (pollen and macrofossil) studies, could further elucidate the establishment history of yellow-cedar in the region. Linking population age structures and pulses of successful regeneration to past climate could explain if locally cold and snowier conditions do favor yellow-cedar reproduction.

Although we believe we located the majority of the yellow-cedar occurrences present within the study area, confirmed by our helicopter survey, it is possible that there are other yellow-cedar trees within the study area, especially in relatively underexplored and inaccessible locations. If future mapping efforts or improved remote sensing technologies located additional yellow-cedar in the study area, habitat modeling efforts in this study could be improved with increasing sample size.

#### *Yellow-Cedar Landscape Distribution*

Topographic, snow, and wind exposure metrics for the 41 yellow-cedar occurrences suggest that yellow-cedar can tolerate a wide range of local environmental conditions; this agrees with broader scale

distribution patterns (Buma, Hennon, et al. 2016) as the yellow-cedar range spans approximately 20 degrees of latitude and a diversity of climatic conditions. Yellow-cedar show a preference for north-facing slopes, but also occur in some south-facing areas (Figure 1.2). North-facing slopes generally retain more snow in the winter, potentially serving as protection from Sitka black-tailed deer and moose which are known to browse yellow-cedar seedlings in winter (Hennon et al. 2016) and from late season soil freezing events (Schaberg et al. 2011). However, we did not see significant differences for any of the three snow variables examined. The lack of a snow signal could be explained by the location of our study at the northeast range edge where yellow-cedar individuals are not yet showing any signs of freezing injury; it is likely that the entire landscape at the northern edge has been snowy enough for yellow-cedar, particularly during times of past establishment. Therefore, yellow-cedar stands might not tend towards snowier portions of the landscape as they would farther south in the range. Also, the MODIS snow record available for analysis only spans the period from 2001 to 2014, which was a generally snowy period in the Gulf of Alaska region (NOAA 2016). Lower snow years, like those projected for the future, may begin to influence where yellow-cedar can persist on the landscape.

Yellow-cedar in the study area are also located in relatively wind sheltered areas, related to their tendency towards north-facing slopes which protect those areas from the prevailing south-southeast storms (Buma and Barrett 2015). We originally hypothesized that yellow-cedar stands might tend towards more disturbance prone portions of the landscape because they are slow growing and relatively shade intolerant compared to the forest dominants in the region (Martin et al. 1995). However, these populations do not appear to be in disturbance prone portions of the landscape, and tree cores from co-dominant species (n = 20; unpublished data) indicate that yellow-cedar are generally surrounded by older western and mountain hemlock and Sitka spruce trees, consistent with similar observations at the northwest range edge in Prince William Sound (Hennon and Trummer 2001). Therefore, yellow-cedar likely did not require a stand-replacing disturbance to establish, but instead appears to have invaded existing forest communities during the Little Ice Age, potentially through small canopy gaps.

The distributions of yellow-cedar occurrences and null points were not significantly different for CTI, but yellow-cedar achieved its highest density at CTI values of ~5.0, representing moderately wet habitats which are known to be yellow-cedar's peak competitive niche in southeast Alaska (Hennon et al. 1990, D'Amore et al. 2009). Most of the mapped yellow-cedar occurrences in this study are located in forested wetlands or well-drained forests adjacent to wetter peatlands. It is possible that this relatively shade-intolerant, but poor-drainage-tolerant, species is able to colonize open-canopy peatlands and then spread into adjacent closed canopy forests when canopy gaps open. We did not analyze soil type

in this study because comprehensive soil surveys are currently lacking for much of the study area; however, we would expect that soil type might have some control on establishment patterns and should be considered in future studies of yellow-cedar migration and establishment.

Although we do not consider biotic factors such as competition, seed dispersal, or reproductive capacity of yellow-cedar in this study, the homogenous forests in the region dominated by the same few tree species (Alaback 1982, Martin et al. 1995) suggest that competition may only control species presence at the fine-scale niche level. Certain forest types currently lacking yellow-cedar in the region are noted to have the same soils and understory plant associations as yellow-cedar-dominated communities, with the lack of yellow-cedar being the only fundamental difference (Martin et al. 1995). Our landscape analyses, reported tree ages, and the location of the study at yellow-cedar's northeast range edge suggest that yellow-cedar's natural migrational history may be responsible for its currently limited presence in the study area at the landscape level rather than environmental constraints.

#### *Habitat Modeling*

We chose to use two complementary approaches to approximately bracket potential yellow-cedar habitat on the landscape because the species appears to have not reached climatic equilibrium in the region. The first approach, in which we included all landscape values where yellow-cedar currently occurs as potential habitat, is likely too generous because it does not account for biotic factors like yellow-cedar's reproductive capacity, dispersal distance, and competition with other species. Additionally, we are currently missing potentially important abiotic factors (i.e., soil type) which were not available across the study area. However, this approach does represent yellow-cedar's fundamental landscape where it is capable of growing and generally illustrates that there are large portions of the landscape topographically and climatically similar to areas currently supporting yellow-cedar at the range edge. Yellow-cedar's occupancy of a wide range of habitat in the study area is consistent with genetic studies that point to yellow-cedar as a climate generalist (Hennon et al. 2016) and the fact that farther south and west in more contiguous parts of its range, yellow-cedar occupies much more of its fundamental landscape niche (Martin et al. 1995).

In contrast, the GLM approach is highly conservative and likely under-predicts suitable habitat due yellow-cedar's lagged migration and limited temporal occupancy of the study area. The GLM highlights wind-sheltered north-facing slopes, with moderate water accumulation as areas that are likely to support yellow-cedar. This is consistent yellow-cedar's ecology in southeast Alaska; yellow-cedar appears most competitive in forested wetlands in the region, where its slow growth, longevity, and suite

of decay-resistant heartwood chemicals are likely advantageous (Hennon et al. 1990, Martin et al. 1995, D'Amore et al. 2009, Hennon et al. 2016). Although the GLM highlights areas where we could expect to find yellow-cedar based on its competitive ability, its major drawback is that it does not account for time and non-equilibrium range edge dynamics. Because yellow-cedar appears to have not reached its full climatic niche in the study area, the GLM is likely marking areas as having low potential for yellow-cedar which are completely suitable; the tree is likely adapted to grow in those locations but has not had time to successfully disperse across the study area.

Developing habitat models for a species that hasn't fully occupied its suitable niche on the landscape due to migration lags can be problematic (Johnstone and Chapin 2003, Feurdean et al. 2013). Therefore, both modeling approaches together offer upper and lower bounds by which to understand the potential for yellow-cedar habitat in the study area, with the ultimate answer probably lying somewhere between the two. Adding factors such as soil type and distance from seed sources could improve modeling efforts in future studies.

#### *Vulnerability Analysis*

Substantial areas of yellow-cedar mortality have been observed only 100 km south of the study area (Dubois and Burr 2015) and mortality has been emerging farther north in recent decades. Although large expanses of habitat within the study area are currently suitable, areas of low snow accumulation may become vulnerable in the near future. Low elevation populations within the study area, in particular, are likely to become vulnerable as regional snowpacks are rapidly diminished (Shanley et al. 2015, Hennon et al. 2016). Based on projected mean winter temperatures under a high emissions scenario, two low elevation populations may become vulnerable to decline by 2050, with an additional six mid-elevation populations, and a portion of a seventh, becoming vulnerable to decline by 2070. In all future climate scenarios examined, two high elevation populations will likely remain snowy to 2070. Soil drainage, which is known to be the other leading risk factor for yellow-cedar decline (Hennon et al. 2012), was not considered in our vulnerability assessment of these yellow-cedar populations.

Future modeling efforts which incorporate soil drainage, actual snow forecasts (rather than temperature only), and examine additional potential climate scenarios are necessary to better predict the vulnerability of yellow-cedar in the future (see Hennon et al. 2016). Low elevation populations in the study area, which are easily accessible via the Juneau road system, could be used in future forest health and monitoring projects to detect when yellow-cedar decline might emerge the Juneau area, and

to ultimately determine if the trailing edge of YCD could overtake the leading edge of punctuated expansion into suitable habitat.

Assisted migration and preservation of yellow-cedar in areas that will remain snowy in the future have been recommended as potential conservation strategies for this high value tree (Hennon et al. 2016). Although controversial, assisted migration may be warranted for species such as yellow-cedar that possess limited reproduction and dispersal capacity (Warren et al. 2001, Lazarus and McGill 2014) and are threatened in portions of their range by changing climate. Yellow-cedar appears to be at a period of relative stasis in the study area, with few healthy saplings and seedlings occurring beyond stand edges (Krapek et al., *in prep*), despite a large pulse of successful regeneration and establishment within stands tied to the cooler and snowier Little Ice Age period (Figure 1.3). Experimental plantings outside of yellow-cedar's contiguous range edge are currently growing well (Hennon et al. 2016) and wider planting could be considered if assisted migration is ever implemented for the species.

## Conclusions

Yellow-cedar is an example of a species whose migrational history and present-day dispersal limits have influenced its existing distribution and non-equilibrium dynamics with current climate. Migration lags can have a major influence on a species' occupancy of its current climatic envelope, as well as that species' ability to potentially track rapidly changing future climates. Before presuming that a species has fulfilled its entire climate envelope, occupancy of currently suitable habitat and dispersal constraints should be considered when determining its adaptive capacity under future climate scenarios.

Our findings on the relatively young age of yellow-cedar populations located within the study area and large area of unoccupied, but potentially suitable, yellow-cedar habitat support previous hypotheses that yellow-cedar is undergoing a continued, punctuated natural range expansion in the Lynn Canal region of southeast Alaska, lagging behind suitable climate conditions (Hennon et al. 2016). Yellow-cedar populations tend towards north-facing slopes, which likely retain snow in winter time and potentially offer protection from both root freezing and deer browse. Additionally, yellow-cedar populations are located in relatively wind sheltered areas, and appear to have initiated within existing hemlock-dominated forests in the study area rather than having required a stand-replacing disturbance to become established.

Yellow-cedar has taken >675 years to occupy only 286 ha of 37,797 ha, or < 0.8 percent, of its fundamental landscape niche in the study area based on our modeling approach that considers the



range of values for landscape variables where yellow-cedar currently grows. Yellow-cedar is an extremely long-lived and stress tolerant tree that may employ a strategy of persisting on the landscape and “waiting” to take advantage of periods of favorable climate or forest composition to reproduce, leading to a pulsed migration following the Last Glacial Maximum. Yellow-cedar’s punctuated migration in the region, partial occupancy of currently suitable habitat, presently limited dispersal capacity, and future reductions in the winter snow regime should all be considered when planning for the conservation and management of this regionally important, high value tree.

Figures

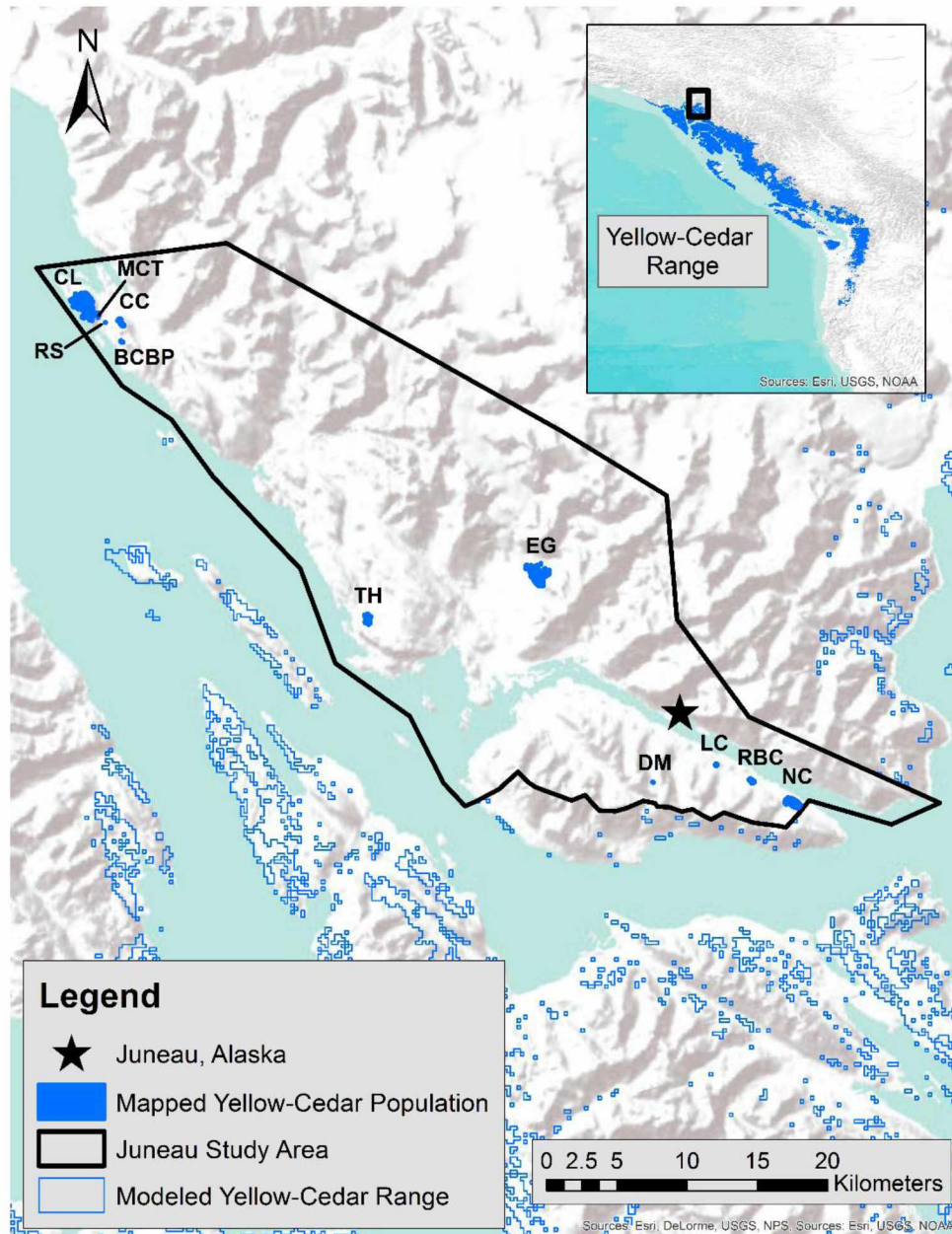


Figure 1.1 Mapped yellow-cedar populations in study area near Juneau, Alaska. Map inset shows study area location in context of yellow-cedar's range (Ellenwood et al. 2015). The modeled range was clipped out of the study area. A small buffer was added to each population so it is visible at the scale of the full study area. Population abbreviations are included next to each polygon: BCBP = Bridget Cover Beaver Pond, CC = Cowee Creek, CL = Cedar Lake, DM = Dan Moller Trail, EG = East Glacier, LC = Lonely Cedar, MCT = McMurchie Cat Trail, NC = Nevada Creek, RBC = Ready Bullion Creek, RS= Roadside, TH = Tee Harbor Ridge.

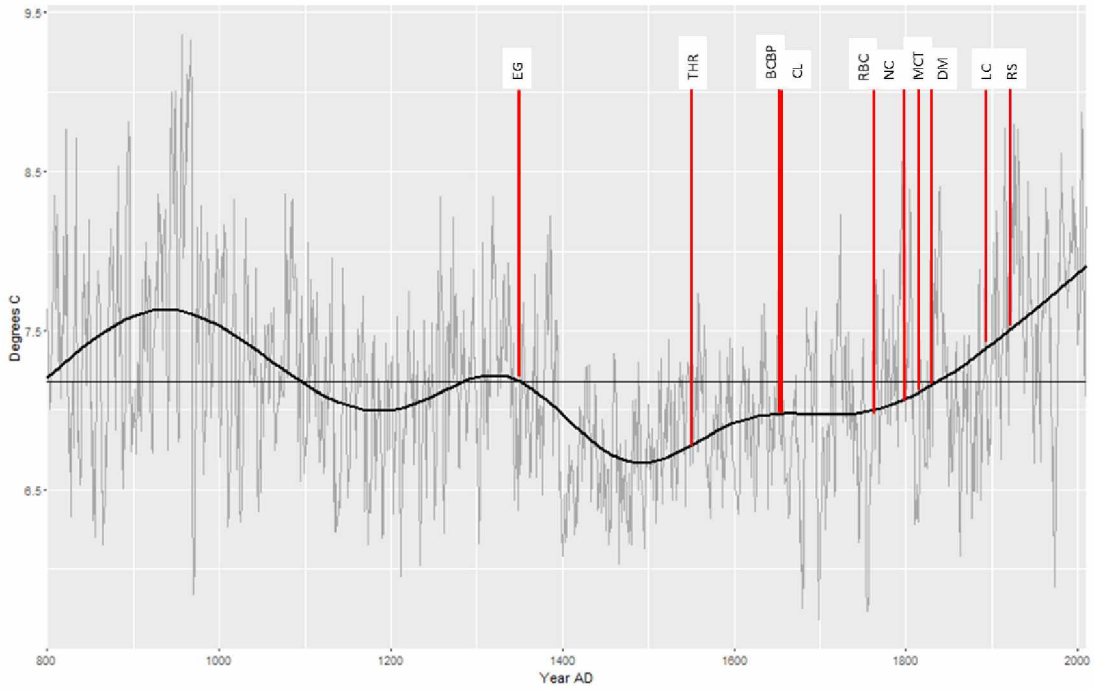


Figure 1.2 Estimated ages recorded for 10 yellow-cedar populations, overlaid with reconstructed temperature for the Gulf of Alaska Region from Wiles et al. (2014). A locally smoothed regression line was added for display of temperature trends. Ages reported are minimum ages (no correction applied for core height or heart rot) and are not necessarily from oldest tree within population; therefore, each population age would be pushed slightly back in time if true ages were determined. Population abbreviations same as Figure 1.1.

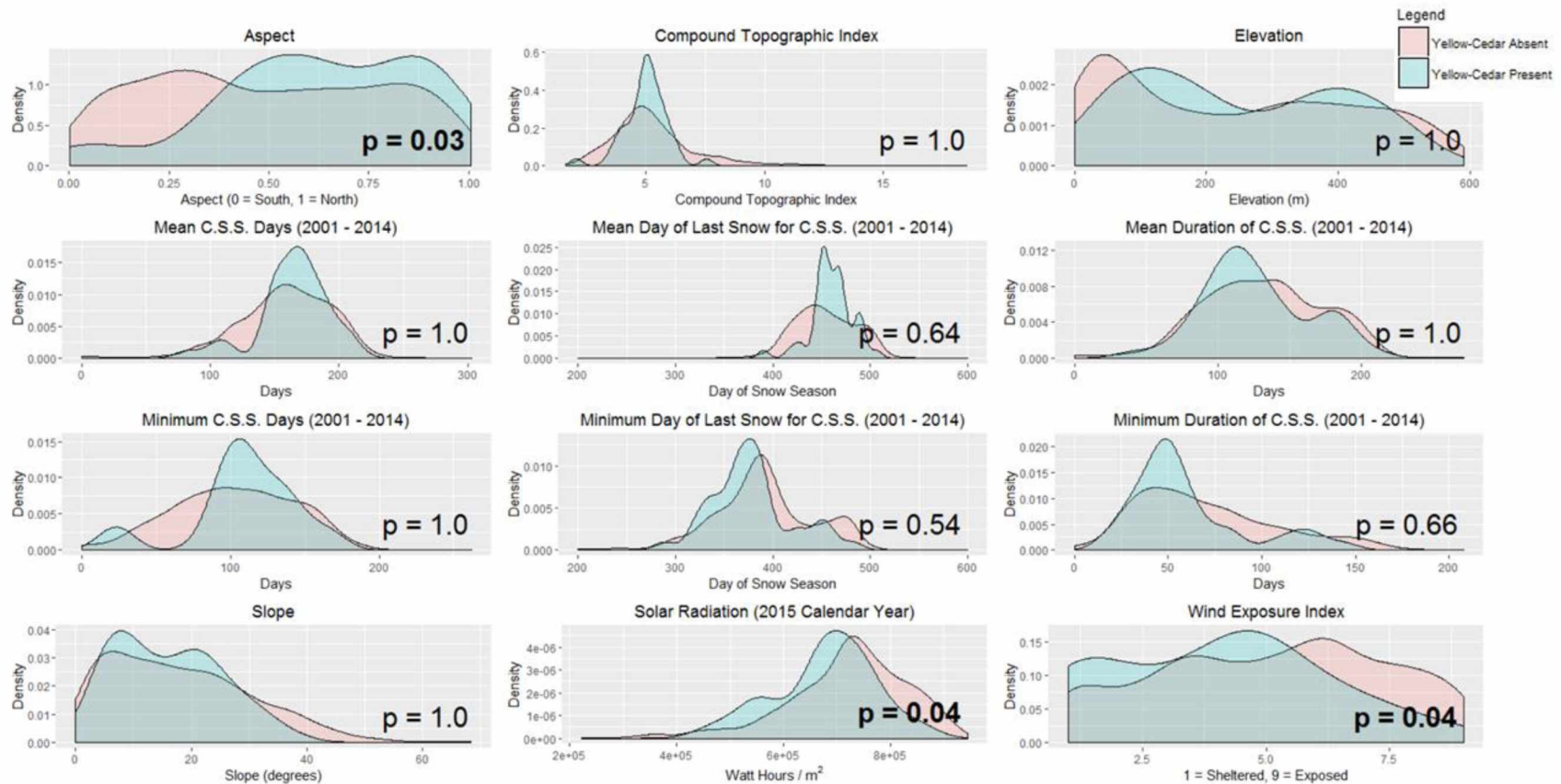


Figure 1.3 Topographic, snow, and disturbance variables for yellow-cedar populations vs. null points. Kernel density plot comparison of topographic variables between yellow-cedar populations and 1,000 null points. Holm-Bonferroni-adjusted Kruskal-Wallis rank sum test p-values in lower right hand corner of each plot; bold indicates significant value ( $\alpha = 0.05$ ). C.S.S. = “Continuous Snow Season”. Note: Day of Snow Season is defined as 1 August to the following 31 July, extending from 213 (Julian DOY for 1 August) to 577 (Julian DOY for 1 August + 365).

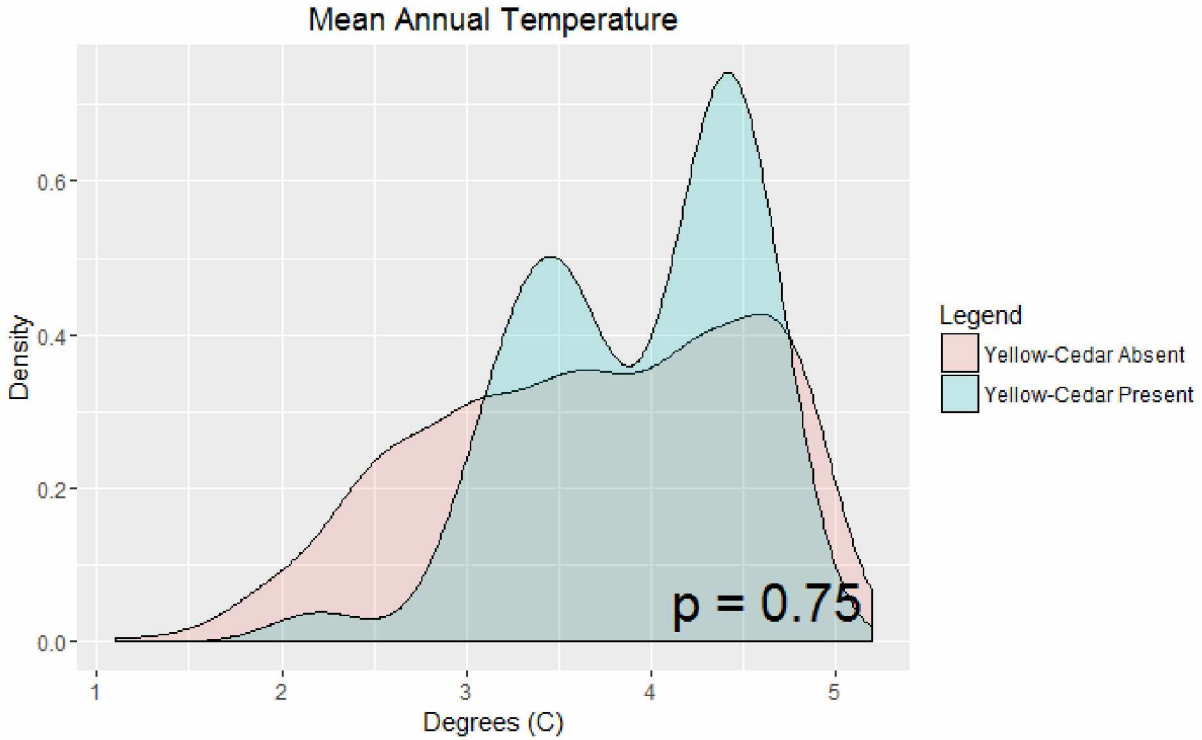


Figure 1.4 Mean annual temperature for yellow-cedar populations vs. null points. Kernel density plot comparing mean annual temperature across yellow-cedar stands and 1,000 null points. Because yellow-cedar occurrences do not differ significantly from the null points in mean annual temperature, elevation is a substantial control on species composition in the study area (Caouette et al. 2016), and elevation is highly correlated with climate variables in the region, we only used elevation in all other analyses. Holm-Bonferroni-adjusted Kruskal-Wallis rank sum test p-value in lower right hand corner of plot. P-Value was adjusted for 13 Kruskal-Wallis tests (12 tests from Figure 1.2 plus this test) to control for the family-wise error rate.

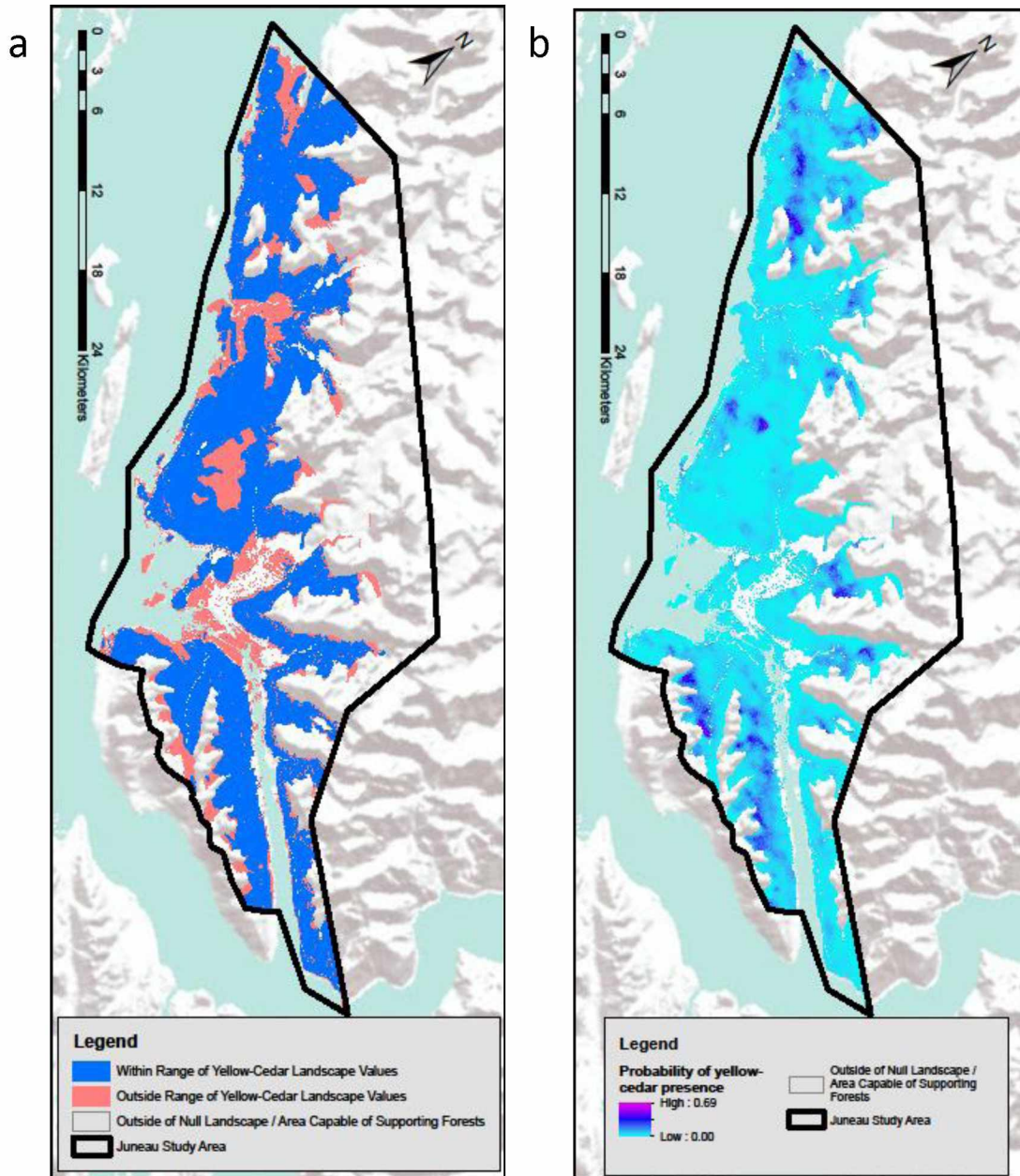


Figure 1.5 Habitat modeling. (a) Potential yellow-cedar habitat in study area based on current landscape areas known to support yellow-cedar. (b) Likelihood of yellow-cedar habitat based on generalized logistic regression of mean landscape values for 41 yellow-cedar occurrences in study area.

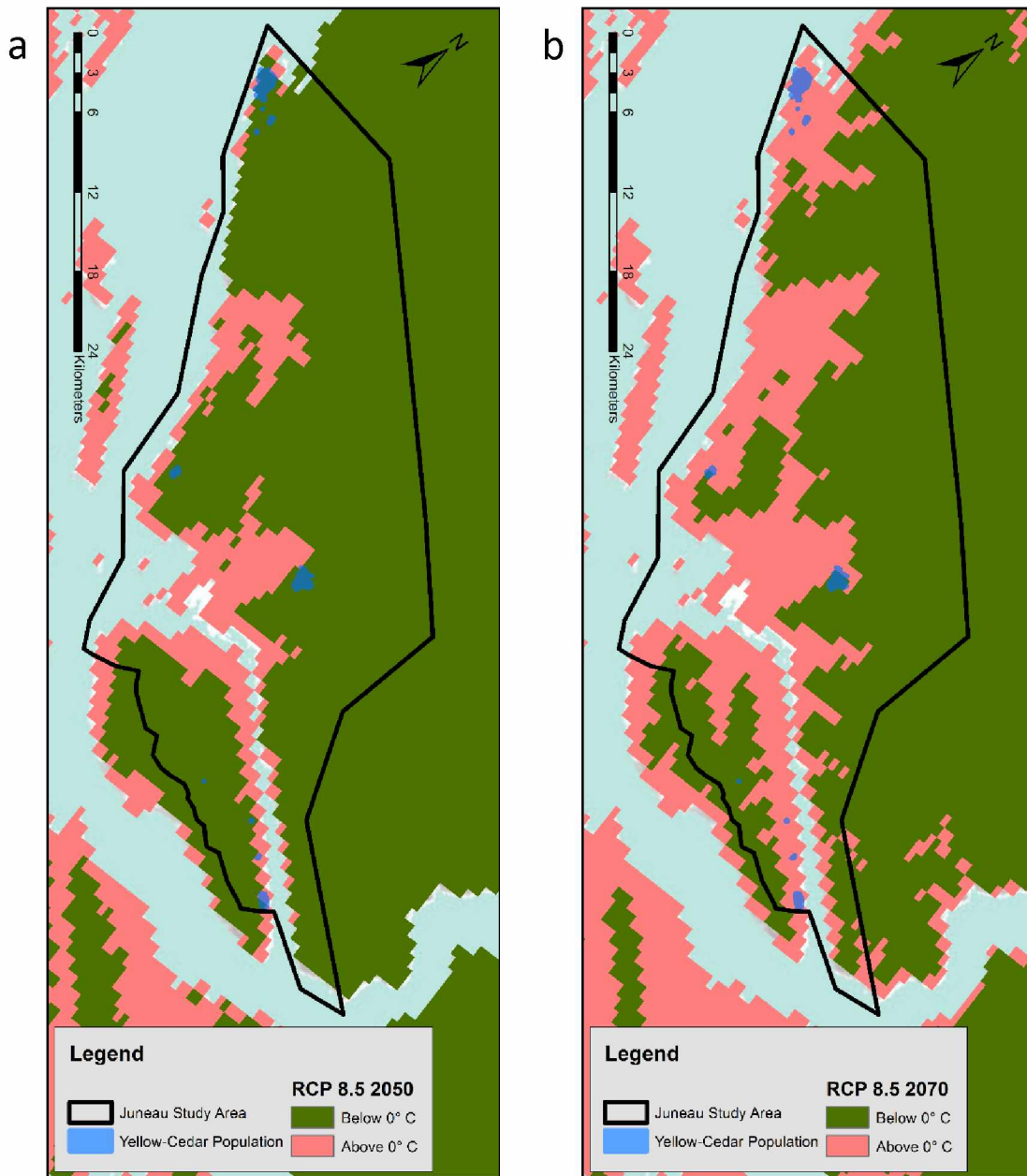


Figure 1.6 Vulnerability analysis. (a) Study area yellow-cedar populations overlaid with mean winter temperature data from the WorldClim HadGEM2-ES RCP 8.5 high emissions scenario in 2050. Note that two low elevation populations lie within the “Above 0°C” mean winter temperature band, indicating potential vulnerability to low snow conditions. (b) Study area yellow-cedar populations overlaid with mean winter temperature data from the WorldClim HadGEM2-ES RCP 8.5 high emissions scenario in 2070. Note that the two highest elevation populations, and portions of a third, maintain a mean winter temperature conducive to a continuous winter snow regime, while all other populations become vulnerable. In the HadGEM2-ES RCP 2.6 low emissions scenario (not shown), all populations remain in the snowy “Below 0°C” band through 2070.

Tables

Table 1.1 GIS data layers and source.

Data Layer	Source
Aspect	
Compound Topographic Index	
Elevation	
Slope	IFSAR DEM; USGS 2015
Solar Radiation	
Mean Annual Temperature	WorldClim; Hijmans et al. 2005
Snow	
Continuous Snow Season Duration	
Day of Last Snow in Continuous Snow Season	GINA; Lindsay et al. 2015
Total Snow Days in Continuous Snow Season	
Wind Exposure Index	Buma and Barrett 2015



Table 1.2 Yellow-cedar occurrence summary statistics.

Population	Occurrence Number (P = Patch, T = Tree)	Area (ha)	Aspect (0=South, 1=North)	Compound Topographic Index (CTI)	CSS Duration Mean (Days)	CSS Duration Min (Days)
Bridget Cove Beaver Pond	P01	0.71	0.60	7.56	139.58	56.40
Bridget Cove Beaver Pond Cedar Lake	P02	0.11	0.91	5.33	139.82	57.85
Cedar Lake	P01	151.72	0.45	5.49	121.91	54.78
Cedar Lake	T01	N/A	0.08	4.46	42.43	17.00
Cedar Lake	T02	N/A	0.07	3.84	128.93	60.00
Cowee Creek	P01	5.71	0.61	5.16	99.01	41.43
Cowee Creek	T01	N/A	0.51	6.18	103.57	42.00
Dan Moller	P01	0.21	0.91	5.51	207.17	144.39
East Glacier	P01	63.78	0.63	5.09	148.61	67.00
East Glacier	P02	0.01	0.86	4.40	98.72	33.67
East Glacier	P03	0.17	0.88	4.67	97.72	34.28
East Glacier	P04	1.07	0.91	4.79	109.00	44.62
East Glacier	P05	0.62	0.44	3.73	125.67	50.70
East Glacier	P06	8.02	0.78	5.00	120.71	50.44
East Glacier	P07	0.04	0.88	4.88	95.12	37.06
East Glacier	P08	0.02	0.78	3.97	92.71	33.22
East Glacier	P09	<0.01	0.86	6.36	92.23	33.00
East Glacier	P10	<0.01	0.87	3.44	98.70	50.67
East Glacier	P11	<0.01	0.37	5.08	160.14	81.00
East Glacier	P12	<0.01	0.41	5.11	113.40	47.00
East Glacier	P13	<0.01	0.51	5.53	113.14	50.00
East Glacier	P14	<0.01	0.51	5.30	118.32	45.00
East Glacier	T01	N/A	0.48	4.96	183.64	83.00
East Glacier	T02	N/A	0.61	2.06	183.64	83.00
East Glacier	T03	N/A	0.59	5.88	115.36	43.00
East Glacier	T04	N/A	0.49	4.84	113.14	50.00
Lonely Cedar	T01	N/A	0.01	4.29	174.57	131.00

Elevation (m)	CSS Last Snow Mean (Day of Snow Year)	CSS Last Snow Min (Day of Snow Year)	Slope (Degree)	CSS Snow Days Mean (Days)	CSS Snow Days Min (Days)	Solar Radiation (wh/m²)	Wind Exposure (1=Low, 9=High)
135.42	446.67	390.93	5.50	165.96	110.21	738350.12	5.13
140.49	446.16	389.85	9.14	165.80	108.40	667640.71	5.01
161.31	447.39	367.98	13.04	159.96	116.21	739561.92	6.28
47.58	390.14	329.00	19.21	81.43	17.00	846587.63	7.33
142.38	465.00	415.00	17.84	171.21	137.00	860639.06	8.33
202.22	417.23	335.57	13.54	160.26	96.31	708966.03	4.60
249.69	425.71	347.00	4.75	163.43	91.00	757979.38	7.33
490.81	506.21	482.00	13.67	213.00	171.00	629837.97	1.11
441.80	475.43	395.02	17.55	189.03	131.50	685333.88	3.34
348.58	457.01	365.00	21.28	153.77	101.67	548786.32	1.00
372.49	456.17	368.09	20.48	152.86	100.16	562295.19	1.00
458.70	462.01	367.31	23.06	166.19	102.77	544379.04	1.00
484.63	466.23	391.60	36.75	168.50	112.99	721079.06	4.97
488.08	464.94	380.25	26.75	169.55	108.26	554721.46	1.64
328.68	453.79	358.59	29.24	147.09	93.12	454032.46	1.00
351.38	452.29	368.11	29.84	146.25	95.33	489397.63	1.00
409.06	452.62	369.00	20.76	146.04	95.00	556705.06	1.45
216.00	471.75	316.33	22.91	147.33	81.33	513864.79	1.00
452.13	470.28	385.33	24.66	201.94	161.00	802651.54	4.67
187.57	468.68	359.00	21.38	170.59	112.00	750982.13	4.42
177.71	469.21	340.00	19.73	167.93	119.00	703003.94	4.33
274.20	468.66	387.00	31.01	177.33	110.00	666758.94	4.13
470.96	489.64	427.00	22.88	205.07	142.00	745877.44	5.00
354.50	489.64	427.00	32.53	205.07	142.00	597990.75	3.67
152.91	467.71	385.00	17.90	176.07	109.00	669912.06	4.33
166.97	469.21	340.00	25.38	167.93	119.00	693240.50	4.33
179.60	468.21	384.00	7.81	190.07	166.00	800855.81	4.67

Table 1.2 continued...

<b>Population</b>	<b>Occurrence Number (P = Patch, T = Tree)</b>	<b>Area (ha)</b>	<b>Aspect (0=South, 1=North)</b>	<b>Compound Topographic Index (CTI)</b>	<b>CSS Duration Mean (Days)</b>	<b>CSS Duration Min (Days)</b>
McMurchie Cat Trail	P01	1.84	0.65	5.35	140.00	61.05
McMurchie Cat Trail	T01	N/A	0.93	5.68	139.86	62.00
Nevada Creek	P01	37.90	0.73	5.72	69.44	20.96
Nevada Creek	T01	N/A	0.96	5.16	78.64	27.00
Nevada Creek	T02	N/A	0.34	5.71	78.64	27.00
Ready Bullion Creek	P01	1.44	0.76	6.16	113.70	47.11
Ready Bullion Creek	P02	0.05	0.87	5.85	120.40	49.00
Ready Bullion Creek	T01	N/A	0.94	3.98	116.00	50.00
Ready Bullion Creek	T02	N/A	0.98	4.69	116.00	50.00
Roadside	P01	0.04	0.37	4.90	141.95	69.64
Tee Harbor Ridge	P01	6.73	0.65	4.96	182.33	114.91
Tee Harbor Ridge	P02	0.04	0.40	5.06	178.77	106.39
Tee Harbor Ridge	P03	5.85	0.64	4.95	181.86	123.05
Tee Harbor Ridge	T01	N/A	0.57	4.13	182.29	123.00

<b>Elevation (m)</b>	<b>CSS Last Snow Mean (Day of Snow Year)</b>	<b>CSS Last Snow Min (Day of Snow Year)</b>	<b>Slope (Degree)</b>	<b>CSS Snow Days Mean (Days)</b>	<b>CSS Snow Days Min (Days)</b>	<b>Solar Radiation (wh/m<sup>2</sup>)</b>	<b>Wind Exposure (1=Low, 9=High)</b>
85.00	454.23	340.59	8.64	173.85	145.56	676345.93	6.29
76.91	456.93	324.00	6.84	178.07	151.00	651988.06	5.33
51.30	429.99	288.03	6.57	100.56	20.96	686059.74	3.03
72.13	447.00	359.00	8.16	111.00	27.00	655369.00	3.00
72.42	447.00	359.00	5.70	111.00	27.00	735863.63	2.00
73.02	450.29	373.48	9.55	149.22	96.45	667179.40	3.36
64.07	451.94	379.00	6.09	153.99	93.50	683797.96	2.78
67.89	451.43	379.00	5.32	151.00	105.00	684504.69	1.67
72.28	451.43	379.00	12.99	151.00	105.00	614876.19	2.00
59.43	453.66	325.82	6.21	178.92	132.73	748828.95	6.36
370.09	489.19	457.90	13.10	187.64	131.88	704196.78	5.83
396.91	486.72	452.22	3.56	186.03	129.89	775959.02	8.92
388.44	488.69	451.91	11.23	188.93	133.60	727852.25	5.20
383.81	488.86	446.00	4.58	186.36	123.00	764156.19	7.00

## References

- Ager, T. A., Carrara, P. E., Smith, J. L., Anne, V., & Johnson, J. (2010). Postglacial vegetation history of Mitkof Island, Alexander Archipelago, southeastern Alaska. *Quaternary Research*, 73(2), 259-268.
- Alaback, P. B. (1982). Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. *Ecology*, 63(6), 1932-1948.
- Beier, C. M., Sink, S. E., Hennon, P. E., D'Amore, D. V., & Juday, G. P. (2008). Twentieth-century warming and the dendroclimatology of declining yellow-cedar forests in southeastern Alaska. *Canadian Journal of Forest Research*, 38(6), 1319-1334.
- Buma, B., Hennon, P. E., Bidlack, A. L., Baichtal, J. F., Ager, T. A., & Streveler, G. (2014). Correspondence regarding "The problem of conifer species migration lag in the Pacific Northwest region since the last glaciation" by Elias, S.A., (2013), *Quaternary Science Reviews* 77, 55–69. *Quaternary Science Reviews*. In press.
- Buma, B., & Johnson, A. C. (2015). Disturbance interactions mediated by topography: Wind exposure, landslide susceptibility, and yellow cedar decline in southeast Alaskan temperate rainforests. *Geomorphology*, 228, 504-511.
- Buma, B., & Barrett, T. M. (2015). Spatial and topographic trends in forest expansion and biomass change, from regional to local scales. *Global change biology*, 21(9), 3445-3454.
- Buma, B., Krapek, J., & Edwards, R. T. (2016). Watershed-scale forest biomass distribution in a perhumid temperate rainforest as driven by topographic, soil, and disturbance variables. *Canadian Journal of Forest Research*, 46(6), 844-854.
- Buma, B., Hennon, P.E., Harrington, C.A., Popkin, J.R., Krapek, J., Lamb, M.S, Oakes, L.E., Saunders, S., & Zeglen, S. (2016). Emerging climate-driven disturbance processes: widespread mortality associated with snow-to-rain transitions across 10° of latitude and half the range of a climate-threatened conifer. *Global change Biology*. In press.
- Burns, R. M., & Honkala, B. H. (1990). *Silvics of North America. Volume 1. Conifers. Agriculture Handbook (Washington)*, (654).
- Caouette, J. P.; Steel, E. A.; Hennon, P. E.; Cunningham, P. G.; Pohl, C. A. & Schrader, B.A. (2016). Influence of elevation and site productivity on conifer distributions across Alaskan temperate rainforests. *Canadian Journal of Forest Research*, 46: 249-261.
- Carrara, P. E., Ager, T. A., & Baichtal, J. F. (2007). Possible refugia in the Alexander Archipelago of southeastern Alaska during the late Wisconsin glaciation. *Canadian Journal of Earth Sciences*, 44(2), 229-244.

- Collins, W. J., Bellouin, N., Doutriaux-Boucher, M., Gedney, N., Halloran, P., Hinton, T., Hughes, J., Jones, C. D., Joshi, M., Liddicoat, S., Martin, G., O'Connor, F., Rae, J., Senior, C., Sitch, S., Totterdell, I., Wiltshire, A. and Woodward, S. (2011) *Development and evaluation of an Earth-System model – HadGEM2*. *Geoscientific Model Development*, 4 (4). pp. 1051-1075. ISSN 1991-9603 doi: 10.5194/gmd-4-1051-2011
- Cronn, R. C., Jennings, T. N., Hennon, P. E., & D'Amore, D. V. (2014). Development of DNA tools to aid genetic conservation and restoration in Alaska yellow-cedar. Final report, U.S. Forest Service Special Technology Development program. Fairbanks, AK: U.S. Department of Agriculture, Forest Service, Alaska Forest Health and Protection Office. 64 p.
- D'Amore, D. V., Hennon, P. E., Schaberg, P. G., & Hawley, G. J. (2009). Adaptation to exploit nitrate in surface soils predisposes yellow-cedar to climate-induced decline while enhancing the survival of western redcedar: A new hypothesis. *Forest Ecology and Management*, 258(10), 2261-2268.
- Davis, M. B., & Shaw, R. G. (2001). Range shifts and adaptive responses to Quaternary climate change. *Science*, 292(5517), 673-679.
- Dubois, G., & Burr, S. (2015). FS-R10-FHP. Forest Health Conditions in Alaska 2015. Anchorage, Alaska. U.S. Forest Service, Alaska Region. Publication R10-PR-38. 78 Pages
- Ellenwood, J. R., Krist, F. J., & Romero, S. A. (2015). National Individual Tree Species Atlas. *United States Department of Agriculture, Forest Service, Fort Collins, CO. Available at: [http://www.fs.fed.us/foresthealth/technology/pdfs/FHTET\\_15\\_01\\_National\\_Individual\\_Tree\\_Species\\_Atlas\\_Spread.pdf](http://www.fs.fed.us/foresthealth/technology/pdfs/FHTET_15_01_National_Individual_Tree_Species_Atlas_Spread.pdf).*
- Feurdean, A., Bhagwat, S. A., Willis, K. J., Birks, H. J. B., Lischke, H., & Hickler, T. (2013). Tree migration-rates: narrowing the gap between inferred post-glacial rates and projected rates. *PLoS One*, 8(8), e71797.
- Gessler, P. E., Moore, I. D., McKenzie, N. J., & Ryan, P. J. (1995). Soil-landscape modelling and spatial prediction of soil attributes. *International Journal of Geographical Information Systems*, 9(4), 421-432.
- Hansen, B. C., & Engstrom, D. R. (1996). Vegetation history of Pleasant Island, southeastern Alaska, since 13,000 yr BP. *Quaternary Research*, 46(2), 161-175.
- Harris, A. S., Hutchison, K., Meehan, W. R., Swanston, D. N., Helmers, A. E., Hendee, J. C., & Collins, T. M. (1974). The forest ecosystem of southeast Alaska: 1. The setting. Gen. Tech. Rep. PNW-GTR-012. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 46 p.
- Hennon, P. E., Shaw, C. G., & Hansen, E. M. (1990). Dating decline and mortality of *Chamaecyparis nootkatensis* in southeast Alaska. *Forest Science*, 36(3), 502-515.
- Hennon, P. E., & Trummer, L. M. (2001). Yellow-cedar (*Chamaecyparis nootkatensis*) at the northwest limits of its natural range in Prince William Sound, Alaska.

- Hennon, P. E., D'Amore, D. V., Schaberg, P. G., Wittwer, D. T., & Shanley, C. S. (2012). Shifting climate, altered niche, and a dynamic conservation strategy for yellow-cedar in the North Pacific coastal rainforest. *BioScience*, *62*(2), 147-158.
- Hennon, P. E., McKenzie, C. M., D'Amore, D., Wittwer, D. T., Mulvey, R. L., Lamb, M. S., Biles, F. E., & Cronn, R. C. (2016). A climate adaptation strategy for conservation and management of yellow-cedar in Alaska. PNW-GTR-917. US Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Heusser, C. J. (1960). *Late-Pleistocene environments of north Pacific North America: an elaboration of late-glacial and postglacial climatic, physiographic, and biotic changes* (Vol. 35). American Geographical Society.
- Heusser, C. J., Heusser, L. E., & Peteet, D. M. (1985). Late-Quaternary climatic change on the American North Pacific coast. *Nature*, *315*(6019), 485-487.
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International journal of climatology*, *25*(15), 1965-1978.
- Hille Ris Lambers, J., Anderegg, L. D., Breckheimer, I., Burns, K. M., Ettinger, A. K., Franklin, J. F., Freund, J. A., Ford, K.R., & Krolss, S. J. (2015). Implications of Climate Change for Turnover in Forest Composition. *Northwest Science*, *89*(3), 201-218.
- Homer, C.G., Dewitz, J.A, Yang, L., Jin, S., Danielson, P., Xian, G., Coulston, J., Herold, N.D., Wickham, J.D. & Megown, K. (2015). Completion of the 2011 National Land Cover Database for the conterminous United States—representing a decade of land cover change information. *Photogrammetric Engineering & Remote Sensing*, *81*(5), 345-354.
- Johnstone, J. F., & Chapin, F. S. (2003). Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. *Global Change Biology*, *9*(10), 1401-1409.
- Jovan, S. (2011). Forest structure and function. In: Barrett, T.M.; Christensen, G.A., tech. eds. Forests of southeast and south-central Alaska, 2004–2008, five-year forest inventory and analysis report. Gen. Tech. Rep. PNW-GTR-835. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 33–45.
- Krapek, J., Hennon, P.E., D'Amore, D.V., & Buma, B. Is a climate-threatened tree successfully expanding into suitable habitat at a leading northern range edge? Prepared for submission in Canadian Journal of Forest Research.
- Lazarus, E. D., & McGill, B. J. (2014). Pushing the pace of tree species migration. *PloS one*, *9*(8), e105380.
- Lertzman, K. P. (1995). Forest dynamics, differential mortality and variable recruitment probabilities. *Journal of Vegetation Science*, *6*(2), 191-204.

- Lindsay, C., Zhu, J., Miller, A. E., Kirchner, P., & Wilson, T. L. (2015). Deriving Snow Cover Metrics for Alaska from MODIS. *Remote Sensing*, 7(10), 12961-12985. Snow cover metrics available at: <http://www.gina.alaska.edu/projects/modis-derived-snow-metrics>
- Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, 462(7276), 1052-1055.
- Malcolm, J. R., Markham, A., Neilson, R. P., & Garaci, M. (2002). Estimated migration rates under scenarios of global climate change. *Journal of Biogeography*, 29(7), 835-849.
- Mann, D. H. (1986). Wisconsin and Holocene glaciation of southeast Alaska. Glaciation in Alaska: The Geologic Record. *Alaska Geological Society*. Pages 237-265
- Martin, J.R., Trull, S.J., Brady, W.W., West, R.A., & Downs, J.M. (1995). Forest Plant Association Management Guide: Chatham Area Tongass National Forest. R10-TP-57. USDA Forest Service, Juneau, AK.
- McLachlan, J. S., Clark, J. S., & Manos, P. S. (2005). Molecular indicators of tree migration capacity under rapid climate change. *Ecology*, 86(8), 2088-2098.
- NOAA (2016). Juneau International Airport Climate Data. Available at: <http://pajk.arh.noaa.gov/>.
- Nowacki, G. J., & Kramer, M. G. (1998). The effects of wind disturbance on temperate rain forest structure and dynamics of southeast Alaska. PNW-GTR-421. US Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Ordonez, A., & Williams, J. W. (2013). Climatic and biotic velocities for woody taxa distributions over the last 16 000 years in eastern North America. *Ecology letters*, 16(6), 773-781.
- Ott, R. A., & Juday, G. P. (2002). Canopy gap characteristics and their implications for management in the temperate rainforests of southeast Alaska. *Forest Ecology and Management*, 159(3), 271-291.
- Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918), 37-42.
- Pearson, R. G., & Dawson, T. P. (2005). Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change. *Biological Conservation*, 123(3), 389-401.
- Pearson, R. G. (2006). Climate change and the migration capacity of species. *Trends in Ecology & Evolution*, 21(3), 111-113.
- Peteet, D. M. (1986). Modern pollen rain and vegetational history of the Malaspina Glacier District, Alaska. *Quaternary Research*, 25(1), 100-120.
- Peteet, D.M. (1991). Postglacial migration history of lodgepole pine near Yakutat, Alaska. *Canadian Journal of Botany*, 69(4), pp.786-796.



- Peteet, D.M. (2000). Sensitivity and rapidity of vegetational response to abrupt climate change. *Proceedings of the National Academy of Sciences*, 97(4), 1359-1361.
- R Development Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.r-project.org>.
- Schaberg, P. G., D'Amore, D. V., Hennon, P. E., Halman, J. M., & Hawley, G. J. (2011). Do limited cold tolerance and shallow depth of roots contribute to yellow-cedar decline?. *Forest Ecology and Management*, 262(12), 2142-2150.
- Shanley, C. S., Pyare, S., Goldstein, M. I., Alaback, P. B., Albert, D. M., Beier, C. M., ... & McPhee, M. V. (2015). Climate change implications in the northern coastal temperate rainforest of North America. *Climatic Change*, 130(2), 155-170.
- Stokes, M. A., & Smiley, T. L. (1968). Tree-ring dating. Chicago-London. University of Chicago Press.
- USGS (2015). Alaska IfSAR Digital Elevation Model. Available at: <http://ifsar.gina.alaska.edu/>
- Veloz, S. D., Williams, J. W., Blois, J. L., He, F., Otto-Bliesner, B., & Liu, Z. (2012). No-analog climates and shifting realized niches during the late quaternary: implications for 21st-century predictions by species distribution models. *Global Change Biology*, 18(5), 1698-1713.
- Warren, M. S., Hill, J. K., Thomas, J. A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D. & Thomas, C.D. (2001). Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, 414(6859), 65-69.
- Wiles, G. C., D'Arrigo, R., Barclay, D., Wilson, R. S., Jarvis, S. K., Vargo, L., & Frank, D. (2014). Surface air temperature variability reconstructed with tree rings for the Gulf of Alaska over the past 1200 years. *The Holocene*, 40(2), 198-208.

## Chapter 2: Is a climate-threatened tree successfully expanding into suitable habitat at a leading northern range edge?<sup>1</sup>

### Abstract

In an era of rapid climate warming, there is considerable interest in understanding if species ranges will be able to track climate and shift to new landscapes that meet their adapted environmental tolerances. Because species do not move across the landscape through empty space, but instead have to disperse through existing biotic communities, basic dispersal ecology and biotic interactions are important to understand. Yellow-cedar, a long-lived conifer of the North Pacific Coastal Temperate Rainforest Region, is thought to be undergoing a continued natural range expansion in southeast Alaska. To examine the current dispersal capacity of yellow-cedar in the region, we located eight range edge populations near Juneau, Alaska, and surveyed stand development and spread of yellow-cedar seedlings beyond existing stand boundaries. Regeneration success varies along understory, plant community, and snow cover gradients, and our results support yellow-cedar's previously identified niche in the region of moderately wet, higher light habitats. Despite suitable habitat beyond stand edges, however, stand expansion appears limited in recent decades. Large quantities of seed are germinating within stands and just beyond boundaries, but seedlings are not developing to maturity. Furthermore, large, ~100-200-year-old trees are located abruptly at stand boundaries, indicating population expansion is in a period of stasis with a last pulse during the Little Ice Age climate period. Vegetative regeneration is common across stands, and may be an adaptive strategy for this long-lived tree to persist on the landscape until conditions are favorable for sexual reproduction, leading to an overall punctuated migration and colonization of new landscapes.

### Introduction

Species' ranges are in constant flux as they track ever-shifting biotic and abiotic niches on the landscape through time (Brown et al. 1996). In an era of unprecedented climate warming, there is heightened interest in understanding if geographic ranges will be able to track future climates, and the implications of geographic range shifts (i.e., expansions, contractions, relocations) for future landscape biodiversity and ecosystem services (Sexton et al. 2009). Biogeographers have examined past range shifts through extensive exploration of the fossil record (Peteet 2000, Williams et al. 2002, Van der

---

<sup>1</sup> Krapek, J., Hennon, P.E., D'Amore, D.V., & Buma, B. Is a climate-threatened tree successfully expanding into suitable habitat at a leading northern range edge? Prepared for submission in Canadian Journal of Forest Research.

Knaap et al. 2005), and have leveraged recent developments in molecular DNA techniques in concert with fossil evidence to understand how species may have tracked past periods of environmental change (McLachlan et al. 2005, Cheddadi et al. 2006, Petit et al. 2008). Considerable work in recent years has focused on understanding how current species distributions have already shifted in recent decades at leading and trailing range edges (Parmesan and Yohe 2003, Chen et al. 2011, Zhu et al. 2012) and modeling how species may continue to shift as they respond to ameliorating or worsening abiotic conditions (Morin and Thuiller 2009).

Although a rapidly changing climate will certainly exert a significant influence on species range shifts through changing abiotic drivers, basic population dynamics and biotic factors are also important. Inter- and intra-specific competition or facilitation, reproductive capacity of populations, dispersal ability, and evolutionary change will all influence how species move across the landscape, and will likely interact with changing environmental conditions to determine future distributions (Davis et al. 1998, Pearson and Dawson 2005, Walck et al. 2011). For plant species, most of which must disperse into new habitats via seeds that possess a limited package of resources, understanding how those seeds will be able to germinate, grow, and compete under novel environmental conditions will be critical to characterizing the invasibility of potential habitat (Davis et al. 2000, Ibáñez et al. 2009, Walck et al. 2011). Studying patterns of plant recruitment at a current leading or trailing range edge can answer questions about these biotic factors in the context of where changing abiotic conditions may also have the largest influence.

Yellow-cedar (*Callitropsis nootkatensis*), a long-lived conifer of the North Pacific Coastal Temperate Rainforest (NPCTR) region, is an example of a species whose dispersal abilities, biotic interactions, and climate sensitivities will interact to shape potential future distributions (Hennon et al. 2016). Yellow-cedar is hypothesized to be undergoing a continued natural range expansion at its northern margin in the Gulf of Alaska region (Hennon et al. 2012, Buma et al. 2014), where it appears to be episodically infilling abundant available habitat on landscape exposed by the retreat of ice since the Last Glacial Maximum (LGM) (Krapek et al., *in prep*). Many of the dominant forest types currently lacking yellow-cedar in the region are markedly similar to yellow-cedar communities in terms of climate, soils, and plant species composition (Martin et al. 1995), as well as disturbance regime (Buma and Barrett 2015), with the lack of yellow-cedar being the only substantive difference. A regional U.S. Forest Service (USFS) plant community publication notes an apparent lack of yellow-cedar in certain local forest types despite what appears to be suitable habitat (Martin et al. 1995). Although tree pollen became present in the regional paleoecological record ca. 13,000 years before present (Hansen and Engstrom 1996), and

climate transitioned to a regime similar to today ca. 4,500 years before present (Heusser et al. 1985, Mann 1986), yellow-cedar pollen only became abundant in central southeast Alaska ca. 2,200 years before present (Ager et al. 2010). Disjunct yellow-cedar populations in Prince William Sound, Alaska, approximately 500 km northwest of yellow-cedar's current contiguous range edge, appear young, healthy, and regenerating well despite growing in a cooler climate (Hennon and Trummer 2001). In short, yellow-cedar appears to be an excellent case study for exploring the mechanisms and patterns of range expansion in a warming climate as community, current climate, edaphic, and disturbance conditions all appear to be non-limiting.

Although yellow-cedar grows in multiple forest types in the region and possesses a wide-range of environmental tolerances, as evidenced by its range spanning more than 20 degrees of latitude (Hennon et al. 2016), the species does appear to fill a particular niche on the landscape. In southeast Alaska, yellow-cedar can co-dominate with western and mountain hemlock (*Tsuga heterophylla* and *T. mertensiana*) on stable, moderately to marginally productive sites with poor drainage and/or shallow soils (D'Amore et al. 2009, Hennon et al. 2016). Because yellow-cedar is relatively shade intolerant compared to western hemlock (Harris et al. 1974), it is more competitive in sites with open canopies, and can also become co-dominant where light conditions (e.g., canopy gaps) allow for successful reproduction in closed canopy forests (Martin et al. 1995). Yellow-cedar reproduces sexually through seed and asexually through vegetative layering. Layering is particularly common in open canopy, wet areas, where lower limbs of trees are retained and can be separated from parent plants by organic matter accumulation (Hennon et al. 1990, Hennon et al. 2016). Layering is also common in areas where heavy snow (e.g., treeline) depresses branches. Snow is important for protecting mature yellow-cedar tree roots from winter and spring freezing events (Schaberg et al. 2008, Hennon et al. 2012) and may also provide protection from ungulate browse (Hennon et al. 2016).

Prized for its many cultural uses, high economic value, and ability to persist and provide ecosystem services in marginal habitats (e.g., forested wetlands in the region, treeline farther south in its range) (Hennon et al. 2016), there is much interest in determining how the yellow-cedar range may or may not be able to track future climate scenarios (Krapek and Buma 2015). Recent climate-driven mass mortality (termed yellow-cedar decline) in warmer portions of its range, only ca. 100 km south of its current contiguous northern range edge where this study was located (Dubois and Burr 2015, Buma et al. 2016), is simultaneously raising concerns about the viability of the species in a warmer climate.

## Objectives

The goal of this study was to examine isolated, leading edge yellow-cedar populations nested within a large amount of suitable habitat near Juneau, Alaska, USA (Krapek et al., *in prep*), and determine the rate and mechanisms of population spread into neighboring, undisturbed forests. We sought to answer the following questions:

1. Expansion: Are range edge yellow-cedar populations successfully expanding into existing forests?
2. Biotic Factors: Is yellow-cedar seedling establishment related to overstory and understory plant community composition?
3. Abiotic Factors: Are factors associated with mature yellow-cedar success and community dominance elsewhere (snow cover, hydrology) also associated with seedling establishment?

## Methods

The study area was located near Juneau, Alaska, USA, which lies just beyond yellow-cedar's current contiguous northeast range edge (Figure 2.1). Yellow-cedar is rare in the surrounding forests, with apparently large expanses of unoccupied, but suitable habitat in the region (Martin et al. 1995, Krapek et al., *in prep*).

## Study Area Description

The climate in the study area (Juneau, Alaska) is cool maritime, with mean monthly temperatures range from -2 to 14°C at sea level throughout the year (NOAA 2016), and strong topographic gradients cause significant variability at fine scales. Precipitation is high, ranging from 1,400 to 2,300 mm annually with no summer drought period, leading to a landscape free of large fires and a mosaic of late seral forests, peatlands, and shrublands (Martin et al. 1995). The predominant forest disturbance in the region is localized windthrow of trees of generally <1000 m<sup>2</sup> patches (Ott and Juday 2002, Buma and Barrett 2015).

Tree diversity is low, with western hemlock dominating most of the moderate to well-drained undisturbed locations; mountain hemlock replaces western hemlock in the subalpine zone and in some wetter community types (Martin et al. 1995). Sitka spruce (*Picea sitchensis*) dominates in frequently disturbed areas (e.g., floodplains), with occasional patches of alder (*Alnus* spp.) and black cottonwood (*Populus trichocarpa*). Yellow-cedar, where found, is often co-dominant with the two hemlock species in marginally productive sites. One hypothesis for yellow-cedar spread at this northeastern range edge is

that yellow-cedar is able to colonize poorly drained, open canopy bog habitats where they are more competitive and then slowly spread into existing well-drained forests via seed as canopy gaps open (Krapek et al., *in prep*).

Yellow-cedar regeneration via seed in the region is limited in closed canopy stands and has been described as “uncommon” and “problematic” throughout southeast Alaska in three USFS plant community publications (Pawuk and Kissinger 1989, DeMeo et al. 1992, Martin et al. 1995). Yellow-cedar is relatively shade intolerant and slow-growing compared to sympatric conifers, and may be outcompeted in closed canopy stands (Hennon et al. 2016). Sitka black-tailed deer (*Odocoileus hemionus sitchensis*) and moose (*Alces alces*) are also known to browse one and two year old yellow-cedar seedlings, and ungulate browse is one hypothesized reason for a broadly observed lack of yellow-cedar regeneration in forests (Hennon 1992, Martin et al. 1995, Hennon et al. 2016). Roots of mature yellow-cedar trees and seedlings in the region are known to be dependent upon a winter snowpack for insulation from periodic cold snaps (temperatures  $\leq -5^{\circ}\text{C}$ ) (Schaberg et al. 2008, Hennon et al. 2012). Seedling juvenile foliage may also depend on snow for insulation, as it may be less cold tolerant than mature foliage and therefore vulnerable to freezing and thawing in the winter (Russell et al. 1990, Hawkins et al. 1994).

#### *Plot Location at Stand Edges*

The geographic extent of 11 leading edge yellow-cedar populations in the Juneau study area (every stand we could locate) was mapped in 2014-2015 (Figure 2.1), spanning a wide range of local topo-edaphic conditions (Krapek et al., *in prep*). Edges of populations were delineated based on the location of mature trees (> 1.4 m in height); any immature individuals of yellow-cedar regeneration (< 1.4 m in height) outside of a stand of mature trees were considered separate from the yellow-cedar population and represent expansion into existing non-cedar forests.

At eight of the 11 mapped yellow-cedar populations, we randomly located 300-m<sup>2</sup> plots (30 x 10 m) along the boundary of the population to examine yellow-cedar regeneration and expansion into existing forests (n = 29 total plots). Each plot spanned the boundary of one of the eight yellow-cedar populations, with 150-m<sup>2</sup> (15 x 10 m) of the plot extending into the yellow-cedar population and 150-m<sup>2</sup> (15 x 10 m) of the plot extending outside the yellow-cedar forest (Figure 2.2). At one of the eight yellow-cedar stands where three regeneration plots were located, the interior of the yellow-cedar stand was so small in area (350 m<sup>2</sup>), that the interior portion of the three plots located there would have

overlapped with each other. Therefore, the entire interior portion of the stand was treated as one larger plot (~350 m<sup>2</sup>), leading to only 27 interior subplots total, and 29 exterior subplots (total n = 56 subplots).

Because we located multiple plots at each population, we wanted to ensure that plots located at the same population were spatially independent in terms of seedling spread and expansion (the driving research topic in this study). Moran's I, a measure of spatial autocorrelation, was used to check for spatial dependency of seedling densities across all plots, and found to be insignificant (data not shown) (Diniz-Filho et al. 2003). Additionally, within populations, plots were located an average distance of 321 m from each other (median = 92 m), likely beyond the maximum dispersal distance of yellow-cedar, which possesses relatively heavy seeds with a limited wing (Burns and Honkala 1990). Therefore, although we located multiple plots at eight populations, plots were spatially independent in terms of seedling production.

The locations of all trees (individuals > 1.4 m diameter at breast height (DBH)) and yellow-cedar regeneration (individuals < 1.4 m DBH; includes seedlings and vegetative layering) within plots were mapped from a sub-meter accuracy GPS control point using a laser range finder (TruPulse 360°R, Laser Technology, Inc.) with internal compass. We recorded if regeneration emanated from seed or from vegetative layering of nearby mature individuals; seedlings can be distinguished by immature needle-like foliage in the first few years of growth, while vegetative layering consists of only mature scale-like foliage, and often has an obvious subsurface connection to a mature individual (Hennon et al. 2016). We distinguished first year germinants, based on height and presence of cotyledons, from seedlings surviving past the first year in all plots. In the remainder of the manuscript, first year seedlings are called "germinants" while seedlings making it past the germinant stage are considered "second year plus" seedlings.

Seedling heights were measured on 10 of 29 plots, and used as an indicator of success in maturation towards tree stage. Seedling heights were grouped into four different categories: 0 – 10 cm, 10 – 50 cm, 50 – 100 cm, and 100 – 140 cm. Seedlings in each successive height class were considered more likely to become trees contributing to stand replacement or expansion. The spatial dependency of seedling densities in height classes in these 10 plots were examined using Moran's I and found to be non-significant, indicating spatial independence of this subsample of plots.

### *Stand Development*

Three of the eight stands where plots were located were fully stem mapped (every tree; tree defined as individual > 1.4 m DBH) to examine stand development (Figure 2.3). We constructed

histograms of overstory yellow-cedar tree diameters in the interior subplots and the three fully stem mapped populations, to examine demography at the edge of a yellow-cedar stand vs. a whole stand.

Increment cores ( $n = 21$ ) were taken from the largest yellow-cedar tree observed in 21 out of 27 interior subplots to determine an approximate minimum age of mature yellow-cedar trees at the edges of study populations. Cores were prepared and aged using standard methods (Stokes and Smiley 1968). Corrections were not applied to tree cores for height from base of tree, or rings missed due to internal decay; therefore tree ages reported are minimum ages and represent underestimates of actual age. Additionally, we targeted only the largest trees; large trees are often older, but not necessarily the oldest trees in each population.

#### *Biotic Factors: Plant Community*

For both trees and yellow-cedar regeneration (seedlings and layering), we recorded descriptive and environmental site data outlined in Table 2.1. The dominant understory plant association within a 3 m radius of each tree and individual of regeneration was recorded (Martin et al. 1995) to determine if yellow-cedar established more readily in certain plant communities. Understory plant associations are also useful indicators of fine-scale abiotic conditions. For yellow-cedar regeneration only, we recorded if individuals had browse damage.

#### *Abiotic Factors: Snow and Soil Drainage*

To determine if seedling recruitment varied as a function of typical snowpack, we used the National Park Service (NPS) and Geographic Information Network of Alaska (GINA) snow cover metrics for Alaska derived from the MODIS daily snow product to determine winter snow cover for the study area (500 m resolution; Lindsay et al. 2015). The continuous snow season (CSS) estimates for the 2001 – 2014 snow seasons were used, which represent 14-day or longer snow cover periods which are more ecologically meaningful for yellow-cedar than short snow cover periods (Krapek et al., *in prep*). Some plots were located in the same snow pixel due the coarse resolution of the dataset, even though microsite differences could be present.

To examine if seedling success, and form of regeneration, varied by soil drainage, we computed a compound topographic index from an interferometric synthetic aperture radar (IfSAR) bare-earth digital elevation model (DEM) created by the U.S. Geological Survey, available at a 5 m resolution in the study area (USGS 2015). Compound topographic index (CTI), a measure of water accumulation across the landscape, was computed as:



$$CTI = \ln\left(\frac{a}{\tan(b)}\right) \quad \text{Equation 2.1}$$

where “a” is the upslope contributing area, and “b” is the slope in radians (Gessler et al. 1995). Mean CTI values were computed for each interior and exterior subplot.

### *Statistical Analyses*

#### Seedling Densities

We divided each 300 m<sup>2</sup> plot into its 150 m<sup>2</sup> “interior” and 150 m<sup>2</sup> “exterior” cedar stand components (Figure 2.2), leading to 56 subplots total as described above. This allowed us to determine if there were differences in yellow-cedar regeneration success across stand boundaries and potential spread into unoccupied forest. We calculated regeneration densities per hectare for germinants, second year plus seedlings, seedlings height classes, and seedlings vs. vegetative layering, for each of the 56 subplots. For exterior subplots, we computed the mean, median, and 95<sup>th</sup> percentile distance that seedlings dispersed beyond the stand edge. We used non-parametric Mann-Whitney U tests to determine if the probability of finding more seedlings of each height class was higher in interior vs. exterior subplots ( $\alpha = 0.05$ ).

The most frequently observed plant association in each subplot was assigned to the entire subplot to compare to regeneration densities by understory plant cover. Exterior and interior subplots were compared separately to avoid comparison of lower regeneration densities outside stands with higher densities inside stands. Plant communities were assigned a drainage score, equivalent to the average percentage of poorly-drained soils in the community observed by Martin et al. (1995).

Because regeneration densities were non-normally distributed along the snow cover gradient, with increasing variance at higher snow cover values, we used Spearman’s rank correlation analysis to assess the relationship between snow and yellow-cedar regeneration. Regeneration densities showed a non-linear response to CTI; therefore, polynomial regression was used to test the relationship between CTI and yellow-cedar regeneration.

#### Spatial Relationships among Seedlings and Trees

Hypothesized biotic drivers (e.g., competition or facilitation) of seedling recruitment and success were assessed via the spatial relationships between overstory plant communities and yellow-cedar seedlings, and amongst yellow-cedar seedlings themselves. The Ripley’s K(r) function (Ripley 1977) has been widely used in point pattern analyses to detect deviations from spatial randomness in a point process, such as stem mapped tree data (Moeur 1993). Besag’s L(r) function (Besag 1977) is a variance-

stabilizing transformation of Ripley's  $K(r)$ , which improves interpretation of deviations in a point process from a hypothetical Poisson distribution at different distance lags (Baddeley et al. 2015). We used the  $L(r)$  function in each subplot to test for clustering or regularity among yellow-cedar seedlings (i.e., seedling to seedling). Additionally, we used the intertype  $L_{1,2}(r)$  function, to examine bivariate spatial associations between yellow-cedar seedlings and mature trees (i.e., seedling to tree relationship) of the dominant three species: western hemlock and mountain hemlock in all subplots, and yellow-cedar in interior subplots only. We chose to test for spatial association at 1, 2, 3, and 4 m distance lags, to span a range of short to intermediate distances that could control relationships between seedlings and trees. Testing at additional lags could inflate the chance of Type II error through multiple comparisons (Baddeley et al. 2014), and testing at greater distances would increase edge effects due to small plot size (10 m width) (Baddeley et al. 2015).

Although Sitka spruce was locally common in some plots, it was not tested for spatial association with yellow-cedar seedlings because it was rare across the majority of subplots. Yellow-cedar vegetative regeneration was not tested for spatial association with overstory trees, as it would be positively associated with the mature yellow-cedar individuals from which it originates.

Before testing for spatial association amongst seedlings and trees, we tested the point pattern in each subplot for complete spatial randomness (CSR), or adherence to a homogenous Poisson process, following quadrat testing methods outlined by Baddeley et al. (2015). If a plot's point pattern (e.g., western hemlock trees and yellow-cedar seedlings) was random ( $p > 0.05$ ), we used a homogenous version of the  $L(r)$  and intertype  $L_{1,2}(r)$  functions. If the point pattern was not random ( $p > 0.05$ ), indicating that the intensity of the point process varied through space, we used an inhomogeneous version of each function to test for spatial association. For each test of spatial association, we generated a simulation envelope using 39 Monte Carlo simulations for a null Poisson distribution to compare to the single observed point process, using isotropic edge correction. This led to 40 total evaluations of  $L(r)$  at each lag, and is comparable to a test of statistical significance at a critical value of 0.05 (Baddeley et al. 2014). If the observed value lay above the simulation envelope, the test supported positive spatial association, while if the observed value lay below the simulation envelope, the test supported a negative spatial association (Figure 2.4). If the observed value lay within the simulation envelope, spatial randomness was supported. Baddeley et al. describe Monte Carlo simulation as a conservative method for testing the significance of spatial association when model parameters are estimated from the data. All computations were done using the *spatstat* package in the R programming language (Baddeley et al. 2015).

To allow for comparison of tests of association between different overstory tree species and yellow-cedar seedlings, an index of the strength of spatial association was computed for each test at each lag (1, 2, 3, and 4 m), similar to methods described by Fajardo et al. (2006). The index of association (IA) was only computed for significant tests at each lag. For the IA, if the observed value at a lag lay above the simulation envelope, the IA was computed as:

$$IA = \frac{\text{Observed } L(r)}{\text{Upper Simulation Envelope } L(r)} \quad \text{Equation 2.2}$$

while if the observed value lay below the lower simulation envelope, the IA was computed as:

$$IA = - \left( \frac{\text{Observed } L(r)}{\text{Lower Simulation Envelope } L(r)} \right)^{-1} \quad \text{Equation 2.3}$$

These equations lead to equivalently positive or negative values showing the strength of association (positive or negative) for a test at a particular lag. An example IA calculation is shown in Figure 2.4.

## Results

### *Seedling Maturation and Spread*

Yellow-cedar germinants and second year plus seedlings were observed at lower densities outside of existing stand boundaries ( $p < 0.01$  for both germinants and second year plus; Table 2.2). Yellow-cedar seedlings of any height class (germinant to 140 cm tall, sub-tree sized seedlings) were observed in 21 of 29 exterior subplots, while seedlings were observed in all 27 interior subplots. Yellow-cedar seedlings appear to follow standard rates of attrition for conifer species, with the most germinants per ha on average, and fewer seedlings surviving into each successive life stage (Table 2.2). However, maturing seedlings ( $> 10$  cm in size) were uncommon in both interior (mean = 160 per ha) and exterior (mean = 73 per ha) subplots, with no significant difference in distributions between interior and exterior subplots ( $p = 0.3$ ). Furthermore, sub-tree size (100-140 cm) seedlings were extremely uncommon across all plots, with only 7 and 13 mature seedlings per hectare on average in interior and exterior subplots, respectively, and no significant difference between subplots ( $p = 1.0$ ).

Vegetative regeneration, on the other hand, was very common in interior subplots (1,698 individuals per ha) and predictably less common in exterior subplots (411 individuals per ha). The difference in vegetative densities between interior and exterior subplots was significant ( $p < 0.01$ ). Vegetative regeneration in exterior subplots occurred primarily at the stand boundary, where mature yellow-cedar

from inside the stand branched into the exterior plot (see Figure 2.2), or where maturing seedlings would branch underground.

On average, yellow-cedar seedlings did not disperse far beyond existing stand boundaries, compared to reported dispersal distances for most conifers (Burns and Honkala 1990). The mean dispersal distance from stands into the 29 exterior plots was 4.65 m (Figure 2.2). The median dispersal distance (50<sup>th</sup> percentile) for seedlings was 4.08 m, and the 95<sup>th</sup> percentile distance was 11.43 m. Of these dispersing seedlings, only 13 per hectare, or < 1 per exterior subplot, on average, survived to a mature seedling stage (100 – 140 cm height). In the field, only one seedling was observed beyond the edge of exterior subplots (16.7 m from yellow-cedar stand), indicating that few seedlings are dispersing farther than the distance we examined into currently unoccupied yellow-cedar forests (personal observation). Although the size of our plots could not capture rare, long-distance dispersal events far beyond stand boundaries, population mapping described by Krapek et al. (*in prep*) indicated that there were few instances overall of individual trees or patches of trees that were located far from main population boundaries in the study area.

#### *Stand Development*

Diameters of overstory yellow-cedar trees in the 27 interior subplots (i.e., within 15 m of stand boundaries) are compared to diameters of overstory yellow-cedar trees in three fully stem-mapped stands (see Figure 2.3 for example of full stem map) in Figure 2.5. Yellow-cedar diameter distributions for both interior subplots (i.e., leading edges of stands) and full stands showed a similar reverse J-shaped distribution, with a small number of large trees and a large number of smaller saplings and pole-sized trees. This indicates that yellow-cedar size distributions at stand edges were similar to yellow-cedar size distributions across stands as a whole.

In 21 interior subplots in which the largest yellow-cedar tree observed was aged, trees were 193 years old on average (median = 199 years). The oldest large tree observed in an interior subplot was 383 years, while the youngest large tree was 86 years old. In other words, within 15 m of stand boundaries (length of interior subplots), large 199-year-old yellow-cedar trees are present, indicating that stand boundaries have not moved more than 15 m since the early 1800s (Little Ice Age period; Wiles et al. 2014), on average. No dead yellow-cedar trees were observed outside of plots to indicate past expansion and contraction; yellow-cedar are extremely decay resistant and can stand for ~100 year after death, and therefore we would have expected to see dead trees if stands had contracted recently.

## *Spatial Relationships among Yellow-Cedar Seedlings and between Yellow-Cedar Seedlings and Overstory Trees*

### Seedling to Seedling

Yellow-cedar seedlings were positively associated (i.e., clustered) with one another at 1 m distances in 37.5 percent of subplots, while they were negatively associated (i.e., inhibited) in none of the subplots at this distance (Table 2.3). Thirty remaining subplots (62.5 percent) showed no statistically significant clustering or inhibition, indicating random distributions, at the 1 m lag. Over increasing lag distances, yellow-cedar seedlings show fewer significant spatial relationships across subplots, and become more regularly spaced (inhibited) where significant relationships were observed (Figure 2.6); at 4 m lag distances, 10 percent subplots showed significant clustering, while 6 percent of subplots showed inhibition.

### Seedling to Tree

On the whole, yellow-cedar seedlings were negatively associated with all three dominant overstory tree species in each subplot, including overstory yellow-cedar, at all lag distances. At 1 m lags, yellow-cedar seedlings were negatively associated with adult western hemlock, mountain hemlock, and yellow-cedar trees in 7, 7, and 28 percent of subplots, respectively, while seedlings were positively associated with these trees in 0, 7, and 0 percent of subplots, respectively (Table 2.3). Negative spatial association between yellow-cedar seedlings and overstory trees increased in frequency and strength (Figure 2.6) at increasing lag distances; statistically significant negative associations between seedlings and western hemlock, mountain hemlock, and yellow-cedar trees at 4 m lags were observed in 26, 21, and 20 percent of subplots, while positive associations were observed in only 4, 4, and 7 percent of subplots, respectively. Yellow-cedar seedlings showed the highest proportion of negative associations with adult yellow-cedar trees (28, 41, 28, and 21 percent of interior subplots, at 1, 2, 3, and 4 m lags, respectively) compared to the two hemlocks.

### *Seedling Densities by Plant Community*

The highest seedling densities in interior (mean = 3,433 per ha) and exterior (mean = 1,615 per ha) subplots were observed in the blueberry – menziesia (*Vaccinium* spp. – *Menziesia ferruginea*) understory plant association. The blueberry – menziesia plant community contains only 19 percent of poorly drained soils on average (Martin et al. 1995) and is the second driest plant community observed in this study based on soil drainage estimates (Figure 2.7). Plots dominated by blueberry – menziesia

understory communities also had the highest number of second year plus seedlings in both interior and exterior plots. Understory plant communities dominated by blueberry and skunk cabbage (*Lysichiton americanum*), a plant association in areas of poor soil drainage (65 – 89 percent of soils poorly drained on average; Martin et al. 1995), showed the second highest densities of yellow-cedar regeneration from seed in interior (mean = 1,760 per ha) and exterior subplots (mean = 278 per ha). Seedlings were less common in the *Cassiope* spp. and blueberry – deer cabbage (*Vaccinium* spp. – *Nephrophyllidium crista-galli*) groups, although these community types were observed in few of the exterior and interior plots overall (see “n” on Figure 2.7). Both of these communities are noted by Martin et al. (1995) to have “poor” regeneration potential because of higher percentage of poorly drained soils, and also short growing seasons in high elevation *Cassiope* communities.

Vegetative regeneration, on the other hand, was most abundant (mean = 5,944 per ha) in the two interior subplots dominated by *Cassiope* spp.; this plant association is common in high elevation areas, where snow-loading can lead to increased incidence of vegetative layering in yellow-cedar (Hennon et al. 2016). Vegetative regeneration densities were also abundant in all remaining plant associations in interior subplots (Figure 2.7), except for the blueberry – skunk cabbage association where it was relatively uncommon, but still present (mean = 587 per ha).

#### *Seedling Densities by Snow and Soil Drainage*

Increasing snow cover was not significantly correlated with seedling and second year plus seedling densities in both exterior and interior subplots (Figure 2.8). Vegetative regeneration, on the other hand, was strongly correlated with increasing snow cover in interior subplots ( $p = 0.76$ ,  $p < 0.01$ ), with no significant relationship observed in exterior subplots.

In interior subplots, seedling densities show a significant quadratic relationship with CTI ( $p = 0.03$ ), increasing up to values of 6.5 and then decreasing (Figure 2.9a). Second year plus seedlings show a similar, but marginally insignificant ( $p = 0.06$ ) relationship with CTI in interior subplots. Vegetative regeneration on the other hand, shows the opposite relationship, with higher densities at low and high CTI values ( $p < 0.01$ ), but a decreasing trend overall. No regeneration types show significant relationships with CTI in exterior subplots (Figure 2.9b). Small sample sizes at high CTI values are likely biasing these results, but overall, trends indicate that moderately wet CTI values show the highest seedling and second year plus seedling densities.

## Discussion

### *Seedling Maturation and Spread*

At this northeastern range edge, yellow-cedar appears to be generating adequate quantities of seed to produce thousands of germinants per hectare inside existing stands, and is also successfully spreading seed beyond stand boundaries (765 germinants per hectare in exterior plots) into currently unoccupied forests (Table 2.2). Therefore, seed production and germination, at least in the snapshot of time of this study, do not appear to be limiting yellow-cedar spread, which addresses concerns regarding unknown seed production expressed in recent assessments (Hennon et al. 2016). However, few of these germinants appear to be surviving to maturity, with only 160 and 73 seedlings per ha over 10 cm in height inside and outside of existing yellow-cedar stands, respectively. Far fewer sub-tree size (100-140 cm) seedlings were observed in plots, with only 7 and 13 per ha inside and outside of stands, respectively, indicating maturation failure both inside and outside existing stands. Three regional plant community publications for southeast Alaska all note a similar lack of mature yellow-cedar regeneration from seed in closed canopy forests in recent decades (Pawuk and Kissinger 1989, DeMeo et al. 1992, Martin et al. 1995). One hypothesis proposed for the lack of yellow regeneration in the Alexander Archipelago region of Alaska is high browse pressure by Sitka black-tailed deer (Hennon 1992, Martin et al. 1995, Hennon et al. 2016) and moose (personal observation). We did not observe a substantial percentage of seedlings or vegetative regeneration that had been browsed by deer and/or moose (data not shown), but it is possible that ungulates are removing entire 1<sup>st</sup> and 2<sup>nd</sup> year seedlings, whose foliage is highly palatable, from the forest each fall – spring (Hennon et al. 2016).

Vegetative regeneration from existing yellow-cedar individuals, on the other hand, was common on plots (1,688 per ha in interior subplots on average; Table 2.2), and across a wide range of understory plant community, drainage, and snow conditions. Vegetative regeneration may be a mechanism that allows yellow-cedar to maintain, or slowly increase, its presence on the landscape in periods that are unfavorable for sexual reproduction. Yellow-cedar is a long-lived, stress-tolerant species (Antos et al. 2016) whose long survivorship (Lertzman 1995) may allow it to persist and “wait” for favorable abiotic (e.g., climate) and/or biotic (e.g., canopy gaps, low deer populations) conditions for regeneration. Vegetative reproduction may be a key component to this long-lived conifer’s episodic spread into suitable habitat (Krapek et al., *in prep*), but is not a successful strategy for rapid mid to long distance colonization of new habitat.

On average, yellow-cedar seedlings are spreading 4.65 m into existing forests not currently occupied by mature, overstory yellow-cedar trees. However, as discussed above, few of these seedlings

currently appear to be surviving to maturity (Table 2.2). It is estimated that yellow-cedar require at least seven years to reach sexual maturity (Hennon et al. 2016); at a high-end assumption of full success of every seedling reaching sexual maturity within seven years, and an average dispersal distance of 4.65 m observed in this study, yellow-cedar is spreading into existing forests at the rate of approximately 0.07 km per 100 years, not considering long-distance dispersal. In short, yellow-cedar appears to be moving into existing forests either extremely slowly or in a punctuated manner (e.g., rapid expansion followed by near stasis, as observed here). That we find isolated populations of mature individuals surrounded by non-cedar vegetation suggests the latter.

Species range shifts are often episodic during periods of abrupt climate change (Walther et al. 2002), a well-studied example of which is the rapid migration of tree species following the Last Glacial Maximum (Davis and Shaw 2001, Williams et al. 2002). Wind dispersed trees, like yellow-cedar, are capable of rapid rates of migration (Lazarus and McGill 2014) if forest and/or climate conditions are favorable. This appears to have been the case during the Little Ice Age climate period (1100 – 1850), when most of the yellow-cedar stands in the study area appear to have established (Krapek et al., *in prep*) and when most dominant low elevation yellow-cedar trees in the region appear to have grown to canopy status (Hennon et al. 1990, Beier et al. 2008).

It is possible that site-specific factors such as soil fertility or parent material are also responsible for yellow-cedar's limited expansion beyond current stand boundaries. In other words, populations may have already fully occupied local niches, and expansion of yellow-cedar on the landscape could be limited to colonization in new, discrete portions of the landscape. However, habitat modeling and a pulse of expansion during the Little Ice Age climate period (Krapek et al., *in prep*), in addition to successful experimental plantings in the region where light and snow conditions are favorable (Hennon et al. 2016), indicate that stands have the potential to expand locally, but current climate and/or forest conditions are the limiting factor rather than soils.

### *Stand Development*

Diameter distributions of yellow-cedar trees in stand edge interior plots and three fully stem-mapped stands provide additional evidence for the lack of yellow-cedar spread in recent years. Interior subplots show a similar diameter distribution to fully mapped stands, both of which include a few large overstory trees and a reverse J-shaped diameter distribution, indicative of old growth conditions (Deal et al. 1991). Stand edges appear to have not expanded in recent decades and instead look similar to interior stand conditions; vegetative reproduction and some seedlings are maturing inside existing



stands, but no developing seedlings and small trees are actively extending stand boundaries forward. Additionally, no obvious yellow-cedar mortality is observed outside stand boundaries to indicate past expansion and retraction (Figure 2.10). If these relatively young, range edge populations were continuing to spread into what appears to be suitable habitat (Krapek et al., *in prep*), then we would expect diameter distributions at stand edges to be composed of all small size class trees, with potentially obvious pulses of recent regeneration.

In 21 of 27 interior subplots, 86 – 383-year-old (average = 193 years; median = 199 years) yellow-cedar trees are located within 15 m of stand boundaries; in some cases, these trees are located abruptly at stand boundaries. This indicates that the average stand edge has moved less than 15 m in since the early 1800's, which coincides approximately with the end of the Little Ice Age climate period. Hennon et al. (1990) and Beier et al. (2008) observed that most mature yellow-cedar trees in other southeast Alaska locations regenerated and grew to canopy status during the Little Ice Age, indicating that this was a favorable period for yellow-cedar establishment across the region.

#### *Spatial Relationships among Yellow-Cedar Seedlings and between Yellow-Cedar Seedlings and Overstory Trees*

Yellow-cedar seedlings are strongly clustered with each other at short distances (1 m) in 37.5 percent of subplots examined, while they are inhibited from all overstory tree species at all lag distances (1 – 4 m) when significant spatial relationships were observed (about 20 percent of subplots on average; Table 2.3). Random spatial associations among yellow-cedar seedlings and overstory trees were observed in the most of the remaining subplots, with only a few instances of clustering with overstory trees. Yellow-cedar is known to be relatively shade intolerant compared to sympatric conifers in the region (Harris et al. 1974, Hennon et al. 2016) and therefore may have been negatively associated with overstory tree locations due to shading. At short distances, yellow-cedar seedlings may be clustered with each other in canopy gaps where more light is available, or in favorable microsites for germination. Yellow-cedar seedlings could also be inhibited from overstory trees due to competition for nutrients. The highest incidence of negative association was observed between seedlings and overstory yellow-cedar trees (Table 2.3); yellow-cedar employ a unique nutrient acquisition strategy compared to other conifers in the region (D'Amore et al. 2009) and it is possible that intraspecific competition for nutrients is leading to inhibition of yellow-cedar seedlings from overstory yellow-cedar trees. It is surprising that yellow-cedar seedlings are inhibited from mature, overstory yellow-cedar trees which act as seed sources; competition for light and/or nutrients could be responsible for this pattern.

### *Regeneration Densities by Plant Community*

Regeneration from seed was most common in blueberry – menziesia understories; menziesia is an indicator species for high light conditions in the region (Martin et al. 1995). The fact that the highest seedling densities were observed in higher light understory communities parallels seedlings' negative spatial relationships with overstory trees; seedlings appear to need relatively high levels of light in more open forests and may cluster in canopy gaps in closed canopy stands. Martin et al. also note the blueberry – menziesia plant community to have “good” regeneration potential and a relatively low percentage of poorly drained soils (19 percent) that could impede tree growth. Seedlings surviving past the germinant stage were also most common in the blueberry – menziesia association.

Vegetative reproduction was particularly common in two high elevation, snowy plots with understories dominated by *Cassiope* spp., but was also common across all other plant associations (Figure 2.7). Yellow-cedar seedlings were most common at moderately wet CTI values (Figure 2.9), which is consistent with high regeneration densities in blueberry – menziesia plant and blueberry – skunk cabbage plant communities which range from moderately dry to fairly wet soils (Martin et al. 1995). Yellow-cedar is known to be most competitive in moderately wet, open canopy habitats in southeast Alaska (Hennon et al. 2016), and our observations are consistent with yellow-cedar occupying this niche on the landscape.

### *Regeneration Densities by Snow and Soil Drainage*

We had expected that seedlings, especially those surviving beyond the initial germinant phase, would be more common in areas of high snow cover. Snow is important for protecting the roots of seedlings (and adults) from periodic winter and late spring cold snaps (Schaberg et al. 2008), may offer protection from ungulate browse on highly palatable seedlings (Hennon et al. 2016), and may also be important for protecting less cold tolerant seedling foliage from freezing events (Russell et al. 1990, Hawkins et al. 1994). In this study, we saw no obvious relationship between seedling success and snow cover (Figure 2.8). In fact, seedlings appeared most abundant in interior plots at populations with the least snow; this could be due to increased germination of seeds in lower elevation, warmer plots, even if seedlings may not survive to maturity in these locations. Low snow cover is also associated with a longer growing season, which could increase both fecundity of mature yellow-cedar in those plots, and growth of new seedlings. Although we did not observe snow having a significant benefit for seedlings in this study, ungulate exclusion studies could provide more definitive evidence on snow's ability to

protect seedlings from browsing. Common garden trials in which simulated snow cover is manipulated could also prove useful for testing the freezing tolerance of seedling foliage and its genetic control in the absence of snow.

One limitation of this study is that we only measured seedling heights in a subset of 10 plots, and additionally, that very few maturing (> 10 cm) seedlings were observed in any plot. Therefore, we did not model seedling height classes (our main measure of seedling success towards tree status) against snow cover, or CTI, due to low sample size. Future studies that carefully examine seedling demography and survival across snow and drainage transects would be important to examining the true influence of snow and soil moisture on seedling success and survival. A complete examination of the yellow-cedar reproductive cycle, from flowering to seed production to germination is also warranted to test for other factors leading to low reproductive success in the region (Hennon et al. 2016).

Additionally, at the northeastern range edge observed in this study, where snow may be more abundant and therefore less of a factor influencing yellow-cedar seedling protection than in warmer portions of the range, other factors may be responsible for controlling yellow-cedar regeneration success. Soil fertility, light conditions in the forest understory, decreased competitive ability with existing forest trees due to changing growing season conditions in a warming climate, or a current lack of suitable disturbance regime may all be factors responsible for the shortage of successful yellow-cedar regeneration observed in this study. Experiments in which light, simulated snow cover, and nutrient regimes are varied could provide additional evidence as to what conditions would lead to increased yellow-cedar seedling success in the forest. Seedlings planted at a common garden on a former clearcut within the study area are currently growing rapidly in high light conditions (Hennon et al. 2016); the area has also historically received abundant snow in the winter to offer potential protection from ungulate browse and/or insulation for seedling foliage.

#### *Applicability to Other Systems*

Species range shifts are often episodic, particularly in periods of abrupt climatic change (Walther et al. 2002) and can be rapid when conditions for colonization are favorable. Although many species ranges have already moved poleward and uphill in response to recent climate changes (Parmesan and Yohe 2003), there are serious concerns that most species will not be able to keep pace with anticipated rates of future climate change (Loarie et al. 2009); factors such as dispersal and regeneration capacity (Pearson and Dawson 2005, Walck et al. 2011) and having to migrate into already occupied communities

(Davis et al. 2000, Ibáñez et al. 2009) may limit species spread even if new portions of the landscape become climatically favorable.

Zhu et al. (2012) have shown an overall lack of migration by eastern North American tree species in response to climate using USFS Forest Inventory and Analysis (FIA) data. At an even finer scale (i.e., edges of range edge populations), our study shows that regeneration and expansion at yellow-cedar's leading range edge is lacking, even though potentially suitable habitat is available and climate should be ameliorating. Our results emphasize the importance of examining biotic factors (e.g., competition, dispersal ability) and local site conditions (e.g., favorable microsites for growth) in determining plant species' ultimate migration capacity (Pearson and Dawson 2005). As we try to predict how species may be able to move across the landscape in the future, examining current dispersal at a range edge and current occupancy of the fundamental landscape niche are good starting points.

## Conclusions

This is the first study to quantify northward range expansion in yellow-cedar, which is concurrently experiencing mass mortality in warmer (more southward) portions of its range. In 29 plots established at 8 stand edges, yellow-cedar seedling success and spread beyond stand boundaries is currently limited. Seeds are germinating, but few are surviving to mature heights, and seedlings are not dispersing far beyond current population boundaries. This is consistent with evidence over the past few decades from regional plant community studies that have noted a broad lack of yellow-cedar regeneration in the region, particularly in areas of high deer populations (Pawuk and Kissinger 1989, DeMeo et al. 1992, Martin et al. 1995). Additionally, diameter distributions and ages of mature yellow-cedar trees at population boundaries indicate that stand edges have been relatively static in recent decades to centuries, with relatively old, large trees located directly at stand boundaries. If stands were spreading into what appears to be suitable habitat in the study area, we would expect to see a gradient of large trees near population centers to smaller trees located near at least some expanding stand edges.

Where seedlings were observed, densities varied by understory plant community, with the highest densities observed with high light condition indicator plants (i.e., blueberry-menziesia understories). Seedlings also appear to show negative spatial relationships with the three dominant overstory tree species, including yellow-cedar. Light regime under current canopy conditions may be one factor contributing to yellow-cedar regeneration failure observed in the region. Vegetative regeneration, which was particularly frequent in snowy plots, was also common among all plots. Vegetative

regeneration may be an adaptive strategy that allows yellow-cedar to persist on the landscape in periods that are unfavorable for sexual reproduction. One hypothesis for yellow-cedar spread in the region is that it disperses to moderately wet, open canopy habitats where it is most competitive, and then invades more well-drained adjacent forests when canopy gaps open (Krapek et al., *in prep*).

Because these plots are stem-mapped (data available from authors), there is the potential to re-measure stands at a future date to further monitor regeneration, stand development, and spread into existing forest communities. There is also strong potential to address the question of limited seedling success in experimental settings, including deer enclosure experiments and common garden studies, as well as through more robust studies of seedling demography for yellow-cedar and associated species.

If we considered climate only, it would seem that the yellow-cedar range might be able to shift north into cooler climates, as it contracts further south; however, yellow-cedar spread into suitable habitat at the range edge currently appears limited. This study highlights that a species' dispersal capacity and regeneration success along biotic and abiotic gradients in novel environments are important considerations in ultimately predicting how that species' range may shift in future climate scenarios.

Figures

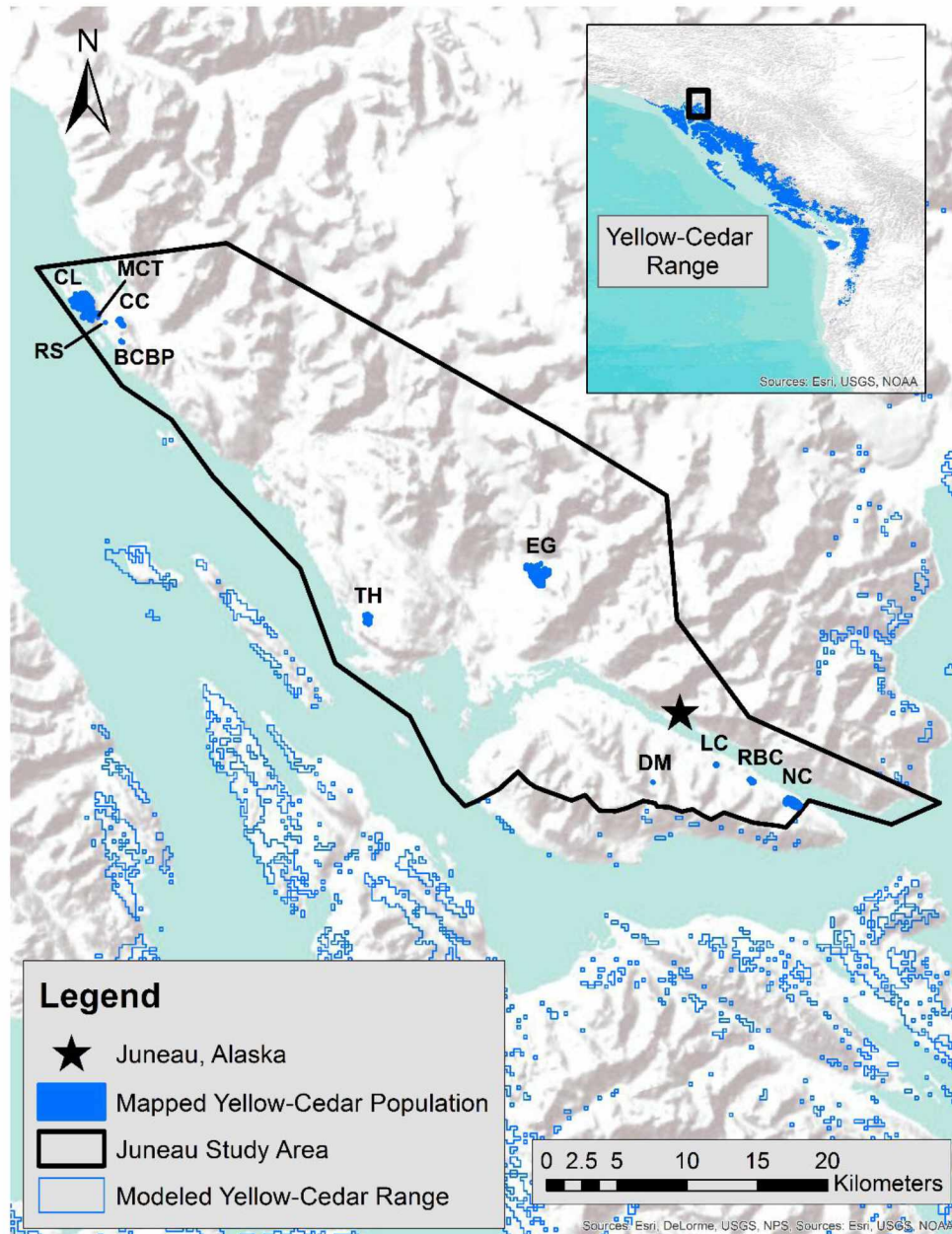


Figure 2.1 Mapped yellow-cedar populations in study area near Juneau, Alaska. Map inset shows study area location in context of yellow-cedar’s range (Ellenwood et al. 2015). The modeled range was clipped from the study area. A small buffer was added to each population so it is visible at the scale of the full study area. Population abbreviations are included next to each polygon. The eight populations used for plot sampling are highlighted in bold: **BCBP = Bridget Cove Beaver Pond**, **CC = Cowee Creek**, **CL = Cedar Lake**, **DM = Dan Moller Trail**, **EG = East Glacier**, **LC = Lonely Cedar**, **MCT = McMurchie Cat Trail**, **NC = Nevada Creek**, **RBC = Ready Bullion Creek**, **RS= Roadside**, **TH = Tee Harbor Ridge**.

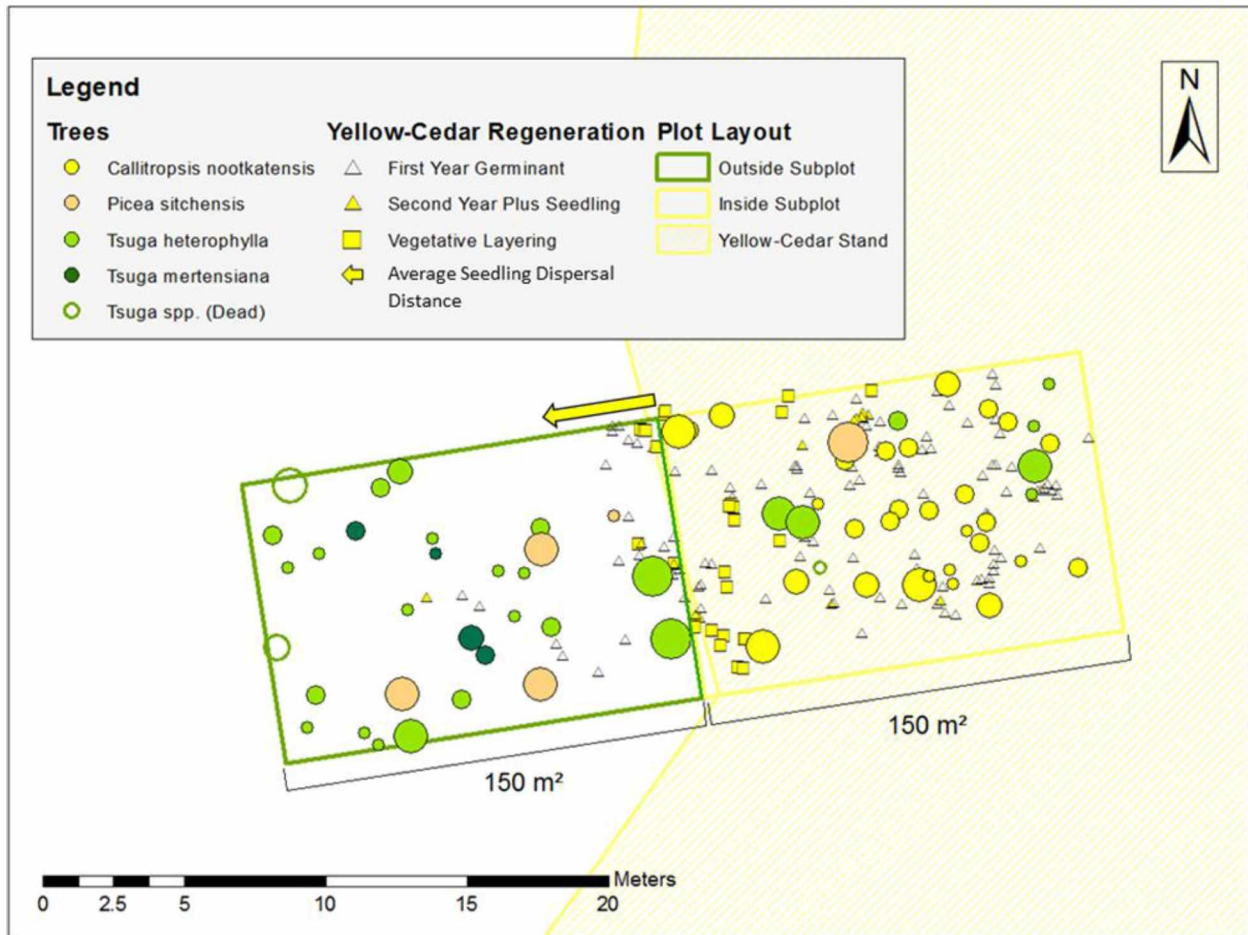


Figure 2.2 Stem map plot layout. Yellow arrow represents the average seedling dispersal distance beyond edge of existing yellow-cedar stand for all 29 exterior subplots. Size of circle corresponds to diameter at breast height measurement for trees. This example plot is located at the Cedar Lake stand shown in Figure 2.1.

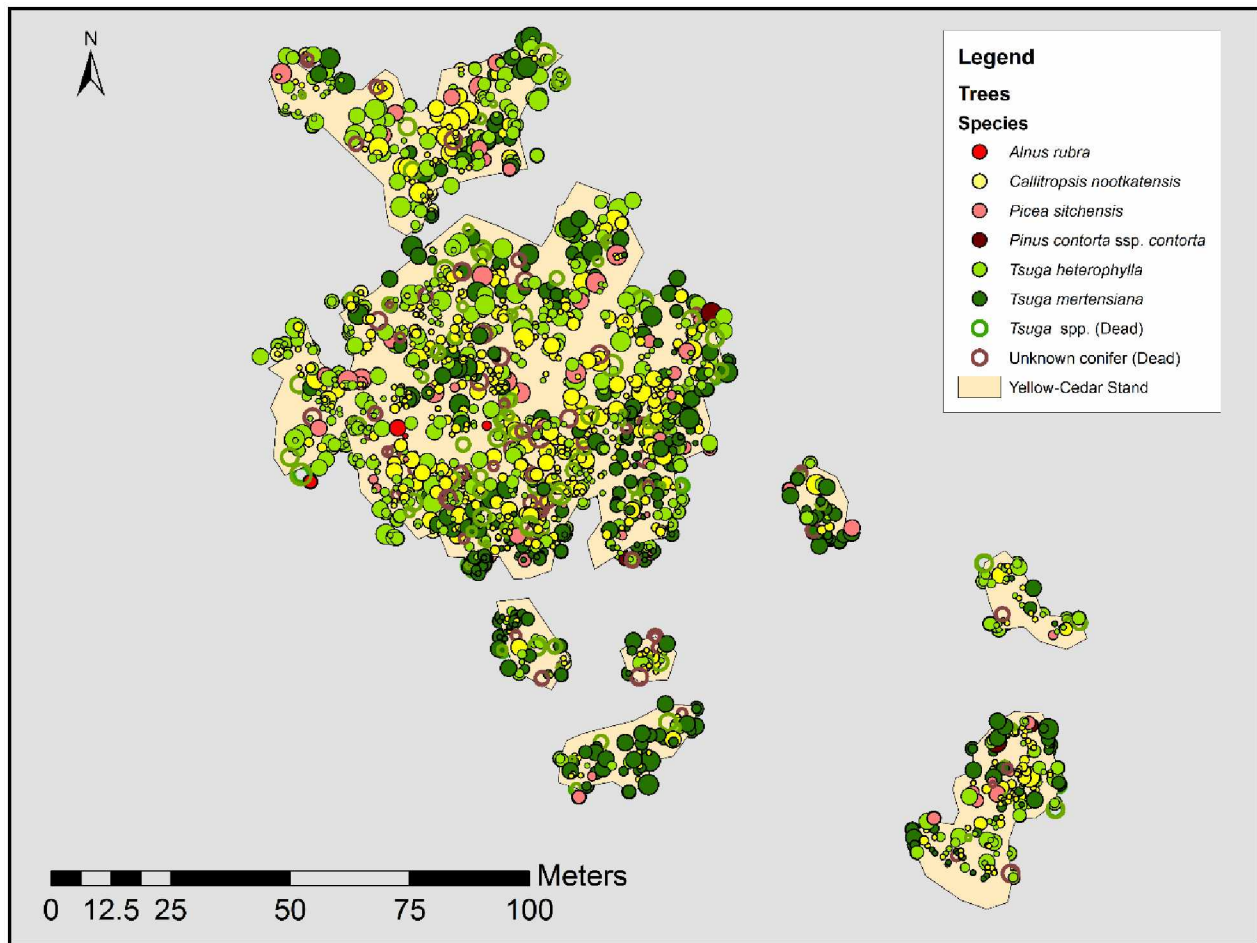


Figure 2.3 Full stand stem map. Example of one of three completely mapped stands, from which full yellow-cedar diameter at breast height (DBH) distributions were compared to interior (edge of stand) subplots. This is the Bridget Cove Beaver Pond stand shown in Figure 2.1.



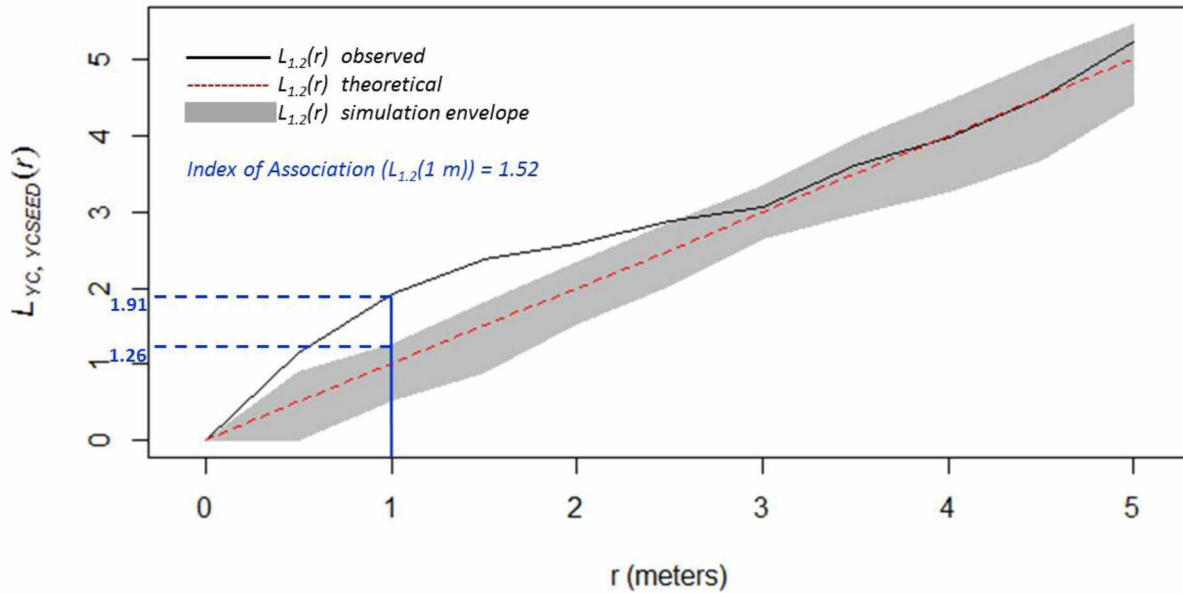


Figure 2.4 Example test of spatial association between yellow-cedar trees (> 1.4 m DBH) and seedlings for one interior subplot. The black line represents the observed  $L_{1,2}(r)$  value, the dashed red line represents the theoretical Poisson  $L_{1,2}(r)$  value, and the grey shaded area represents the upper and lower bounds of 39 Monte Carlo simulations. At  $L_{1,2}(1\text{ m})$ , the observed value shows significant positive association (clustering), as it lies above the simulation envelope. At lags greater than 2.5 meters, there is no significant association between the seedlings and tree locations, indicating randomness. The Index of Association (IA), a measure of the strength of spatial relationship described above, can be used to compare the strength of spatial association among plots and species.

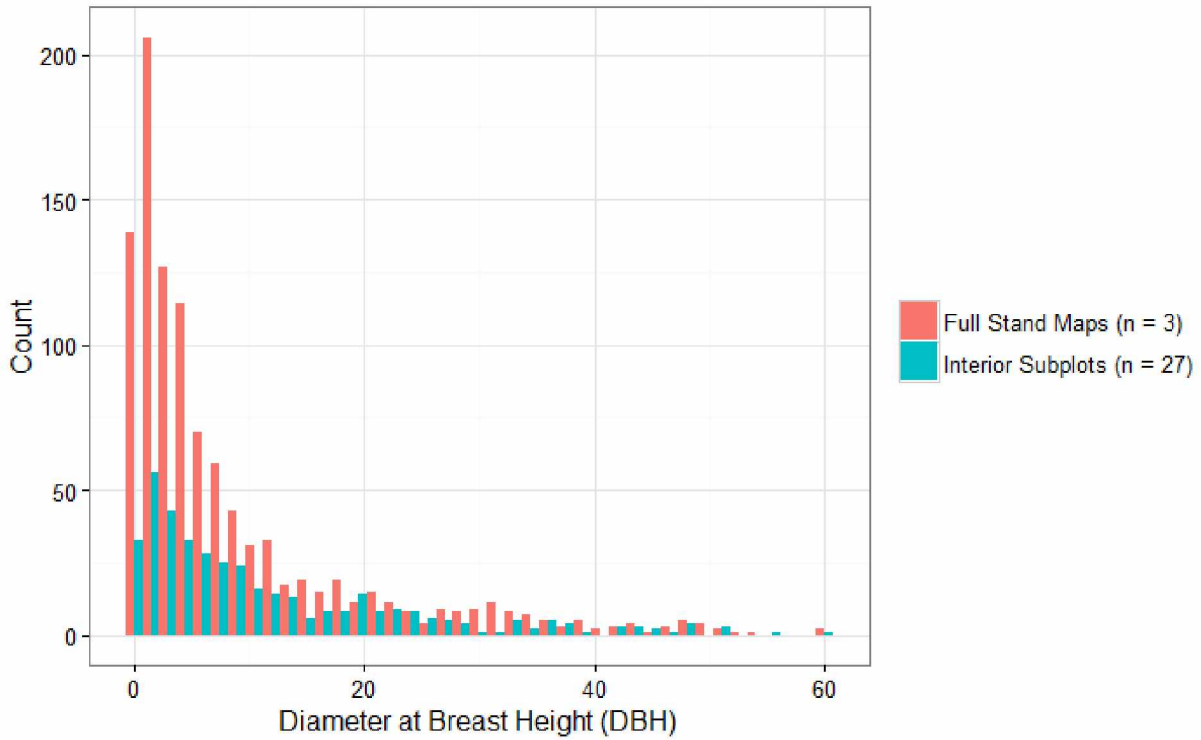


Figure 2.5 Full stand vs. interior subplot DBH distributions. Pooled overstory (> 1.4 m DBH) yellow-cedar diameter distributions for 27 interior subplots and three fully stem-mapped yellow-cedar populations. Trees emanating from vegetative regeneration, when noted, were removed from histograms to reduce bias towards small individuals, as vegetative regeneration on plots tended to consist of small, pole-sized trees next to larger mature adults. Both interior subplots and full stands of yellow-cedar trees follow a similar reverse J-shaped distribution, indicating old growth conditions.

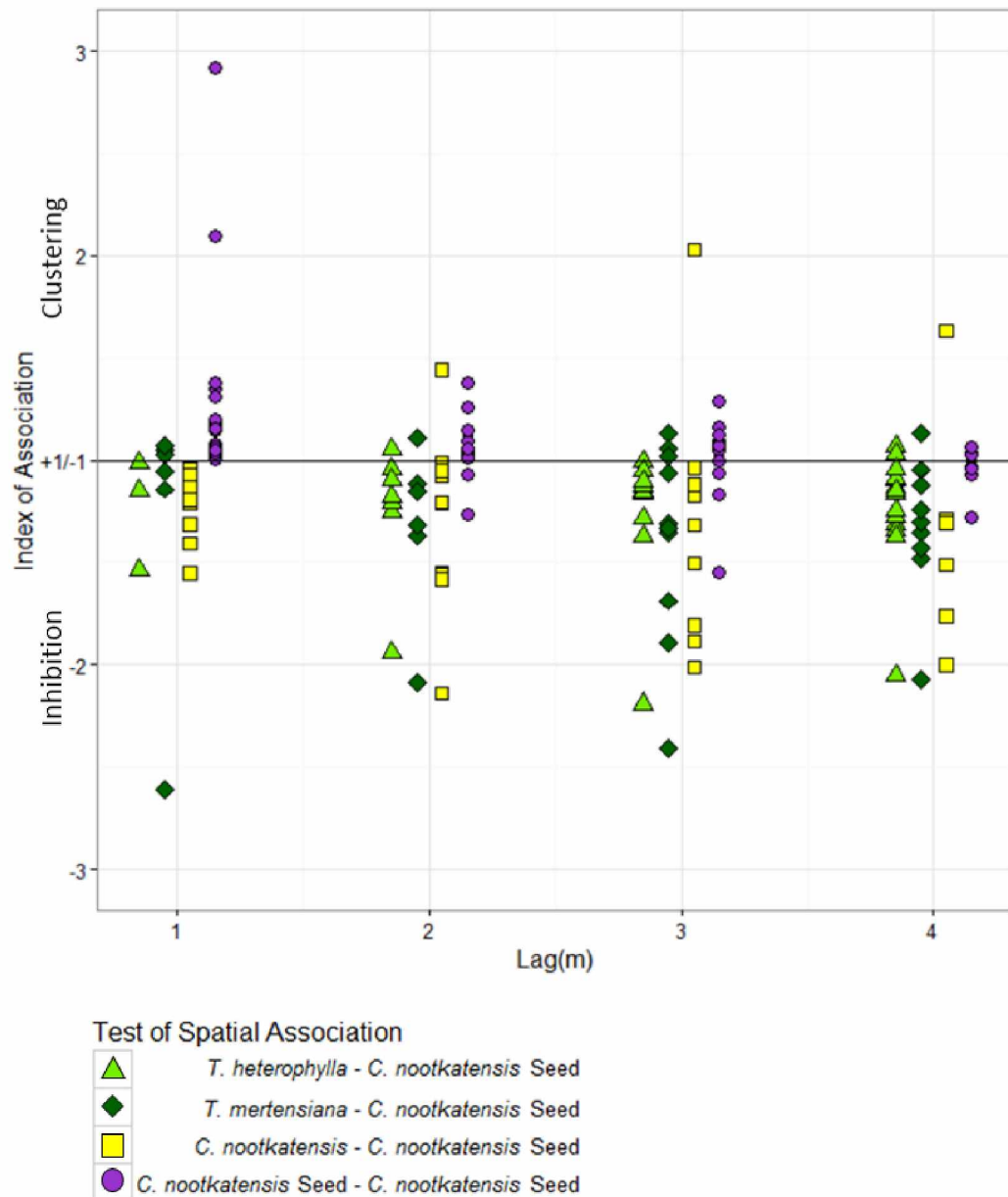


Figure 2.6 Index of spatial association between seedlings and overstory tree species, and between seedlings and seedlings. Spatial associations were tested at 1, 2, 3, and 4 meter lags using Ripley's  $L(r)$  function as described above. For each statistically significant test at  $\alpha = 0.05$ , an index of spatial association (IA) was calculated, which represents the strength of association for the test. Data points falling above the horizontal line at +1/-1 represent subplots showing positive spatial association, while points falling below the line represent negative association. The number of statistically significant tests for each lag is shown in Table 2.3.

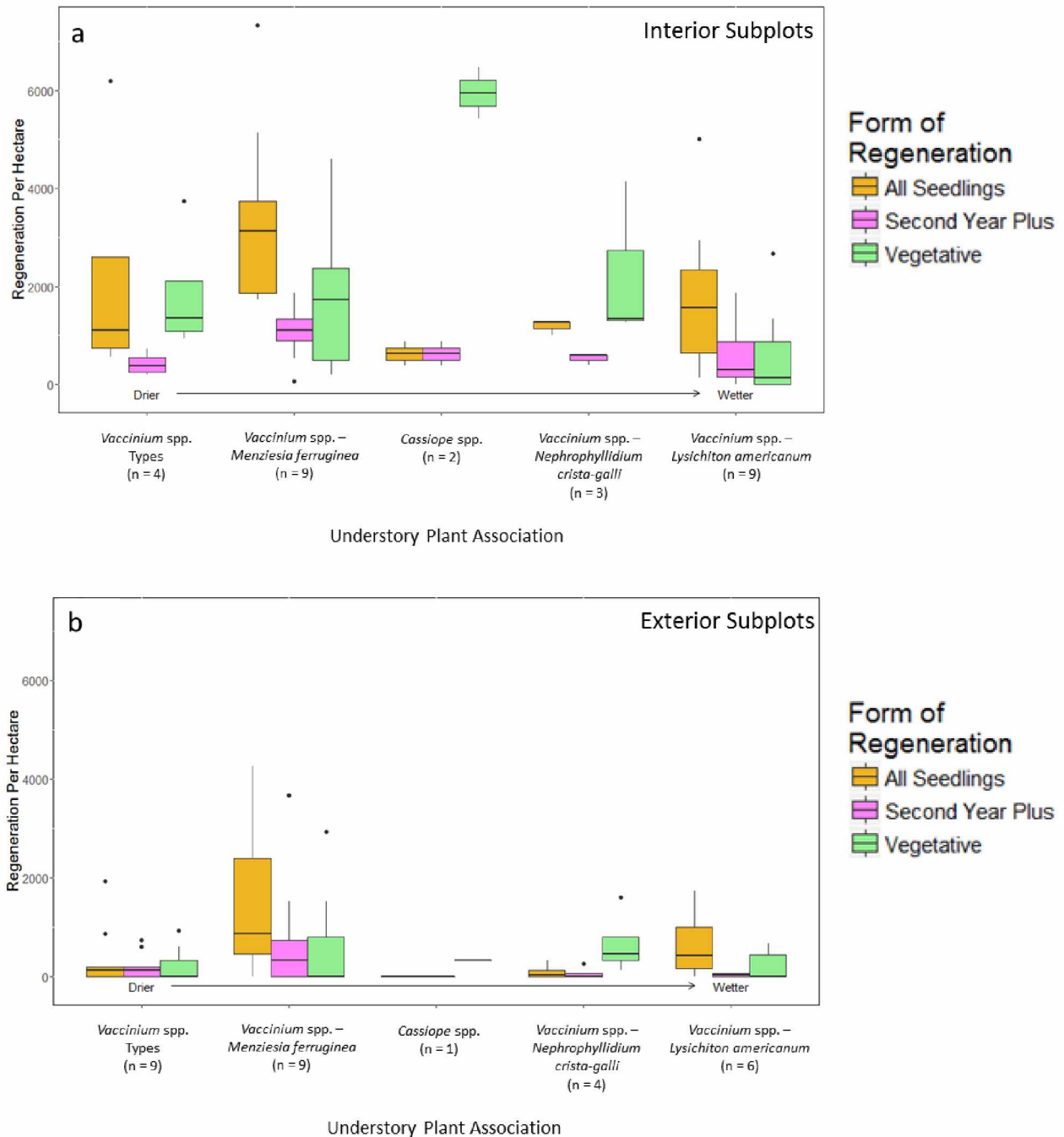


Figure 2.7 Yellow-cedar regeneration densities in understory plant community associations. (a) Interior subplots. (b) Exterior Subplots. Communities are ordered left to right based on soil drainage: communities on left have a higher percentage of well-drained soils, communities on right a higher proportion of poorly drained soils (Martin et al. 1995). Some blueberry (*Vaccinium* spp.) type communities with similar species composition and soil drainage characteristics are lumped together. In one exterior plot, the dominant plant association was devil’s club – skunk cabbage (*Oplapanax horridus* – *Lysichiton americanum*), and this plot was lumped with the blueberry – skunk cabbage (*Vaccinium* spp. – *Lysichiton americanum*) category due to similar composition and soil drainage.

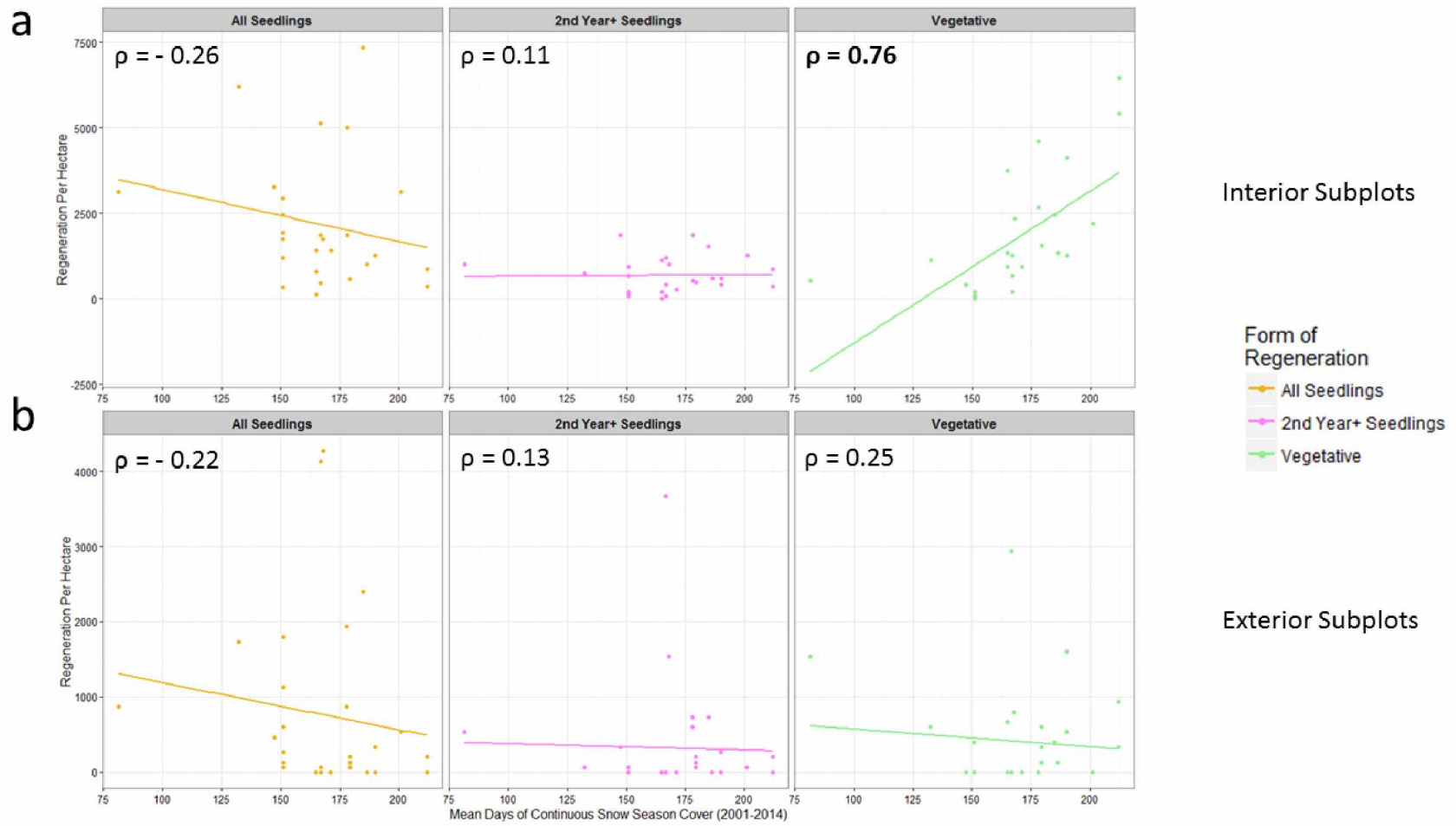


Figure 2.8 Regeneration densities across snow conditions. (a) Interior subplots. (b) Exterior subplots. The x-axis represents the mean number of days providing continuous snow season cover during the 2001 – 2014 snow seasons. Spearman's rank correlation coefficient ( $\rho$ ) is in the top left corner of plots; bold indicates significance at  $\alpha = 0.05$ . A simple linear regression was fitted to points for illustrative purposes only. Note differing y-axis scales in interior and exterior subplots.

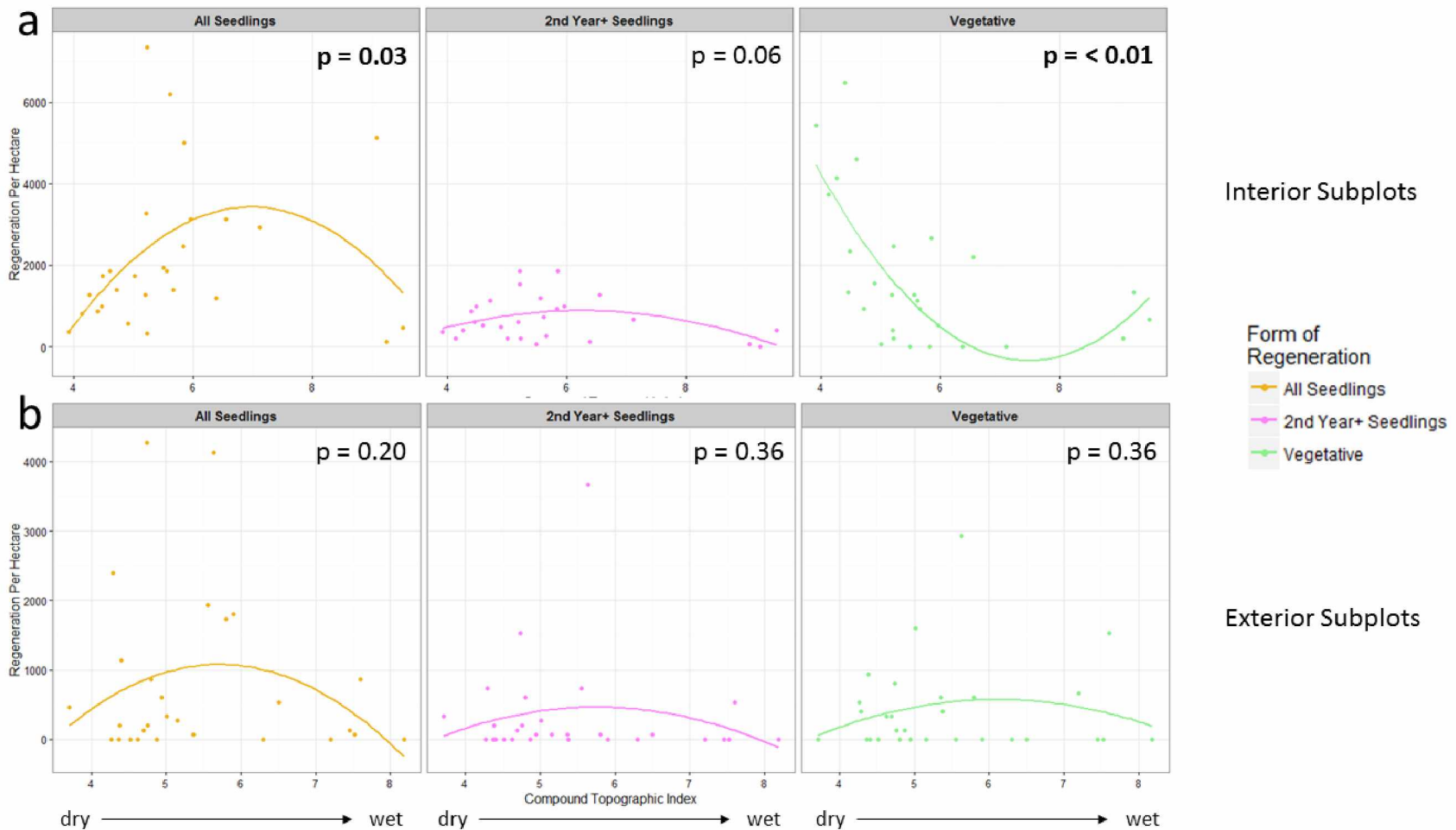


Figure 2.9 Regeneration densities across local hydrologic conditions. (a) Interior subplots. (b) Exterior subplots. The x-axis represents compound topographic index, a unitless measure of water accumulation on the landscape. Quadratic regression model line shown in each plot. The significance level of the quadratic CTI term is shown in top right corner of each plot; bold indicates significance at  $\alpha = 0.05$ . Note differing y-axis scales between interior and exterior subplots.



Figure 2.10 Photograph of a typical yellow-cedar stand boundary in the study area. Approximately 200-year-old yellow-cedar are located abruptly at the stand edge, with regeneration of other tree species outside the boundary, indicating that stands have been in a period of relative stasis for the past many decades to centuries. No obvious yellow-cedar mortality is observed outside the stand boundary. Some stands observed are younger, but many stand edges appear to be in a period of relative stasis.

Tables

Table 2.1 Information recorded for stem-mapped trees and yellow-cedar seedlings

<b>Trees ( &gt; 1.4 m DBH)</b>	
<b>Measurement</b>	<b>Units / Notes</b>
Species	<i>Callitropsis nootkatensis</i> , <i>Picea sitchensis</i> , <i>Tsuga heterophylla</i> , <i>Tsuga mertensiana</i> , unknown <i>Tsuga</i> sp., <i>Alnus viridis</i> , <i>Alnus rubra</i> , <i>Sorbus sitchensis</i> , <i>Malus fusca</i>
Understory Plant Association	Dominant plant association in 3-m radius according to Martin et al. 1995
Diameter at Breast Height (DBH)	Centimeters (cm)
<b>Yellow-Cedar Regeneration ( &lt; 1.4 DBH)</b>	
<b>Measurement</b>	<b>Units / Notes</b>
Understory Plant Association	Dominant plant association in 3-m radius according to Martin et al. 1995
Form	Vegetative or Seed
Deer Browse	Yes or No
Age Class	1 <sup>st</sup> Year Germinant or 2 <sup>nd</sup> Year Plus
Height of Seedlings from Seed*	Centimeters (cm)



Table 2.2 Mean regeneration densities per hectare by subplot type

1 <sup>st</sup> Year Germinants		2 <sup>nd</sup> Year Plus Seedlings		Maturing Seedlings (10 cm+)*		Mature (100 – 140 cm) Seedlings <sup>1</sup>		Vegetative Regeneration (< 1.4 m height)	
Interior (n =27)	Exterior (n = 29)	Interior (n =27)	Exterior (n = 29)	Interior (n = 10)	Exterior (n = 10)	Interior (n =10)	Exterior (n = 10)	Interior (n =27)	Exterior (n = 29)
<b>2,178</b> <sup>2</sup>	765	<b>688</b>	319	160	73	7	13	<b>1,698</b>	411
+/- 1,850	+/- 1,165	+/- 532	+/- 768	+/- 216	+/- 111	+/- 21	+/- 42	+/- 1,778	+/- 659

<sup>1</sup> Seedling heights subsampled on only 10 plots

<sup>2</sup> Bold indicates Mann-Whitney U significance ( $\alpha = 0.05$ ) of interior regeneration density exceeding that of exterior plot.

Table 2.3 Count of positive, negative, and non-significant (random) spatial associations tested.

Lag Spatial Association	1 m			2 m			3 m			4 m			Total Number Tests <sup>1</sup>
	Pos.	Neg.	Non- Sign.	Pos.	Neg.	Non- Sign.	Pos.	Neg.	Non- Sign.	Pos.	Neg.	Non- Sign.	
<i>T. heterophylla</i> Tree	<b>0</b>	<b>3</b>	43	<b>1</b>	<b>6</b>	39	<b>0</b>	<b>11</b>	<b>35</b>	<b>2</b>	<b>12</b>	<b>32</b>	46
<i>T. mertensiana</i> Tree	<b>3</b>	<b>3</b>	37	<b>1</b>	<b>5</b>	37	<b>3</b>	<b>7</b>	<b>33</b>	<b>1</b>	<b>9</b>	<b>33</b>	43
<i>C. nootkatensis</i> Tree	<b>0</b>	<b>8</b>	21	<b>1</b>	<b>12</b>	16	<b>2</b>	<b>8</b>	<b>19</b>	<b>2</b>	<b>6</b>	<b>21</b>	29
<i>C. nootkatensis</i> Seed	<b>18</b>	<b>0</b>	30	<b>9</b>	<b>2</b>	37	<b>6</b>	<b>6</b>	<b>36</b>	<b>5</b>	<b>3</b>	<b>40</b>	48
	<i>C. nootkatensis</i> Seed			<i>C. nootkatensis</i> Seed			<i>C. nootkatensis</i> Seed			<i>C. nootkatensis</i> Seed			

<sup>1</sup>Because no adult *Callitropsis nootkatensis* trees were observed in exterior subplots, tests of association with adult *C. nootkatensis* trees were only performed for interior (n=29) subplots. In 8 of 56 subplots, all of which were exterior subplots, no *C. nootkatensis* seedlings were observed, leading to 48 total subplots tested for association amongst *C. nootkatensis* seedlings. An additional 2 of those 48 subplots had no *T. heterophylla* trees, leading to 46 subplots tested for association between *T. heterophylla* trees and *C. nootkatensis* seedlings. Five subplots had no *T. mertensiana* trees, leading to only 43 subplots tested for association between *T. mertensiana* trees and *C. nootkatensis* seedlings.

## References

- Ager, T. A., Carrara, P. E., Smith, J. L., Anne, V., & Johnson, J. (2010). Postglacial vegetation history of Mitkof Island, Alexander Archipelago, southeastern Alaska. *Quaternary Research*, *73*(2), 259-268.
- Antos, J. A., Filipescu, C. N., & Negrave, R. W. (2016). Ecology of western redcedar (*Thuja plicata*): Implications for management of a high-value multiple-use resource. *Forest Ecology and Management*, *375*, 211-222.
- Baddeley, A., Diggle, P. J., Hardegen, A., Lawrence, T., Milne, R. K., & Nair, G. (2014). On tests of spatial pattern based on simulation envelopes. *Ecological Monographs*, *84*(3), 477-489.
- Baddeley, A., Rubak, E., & Turner, R. (2015). *Spatial Point Patterns: Methodology and Applications with R*. London: Chapman and Hall/CRC Press. URL <http://www.crcpress.com/Spatial-Point-Patterns-Methodology-and-Applications-with-R/Baddeley-Rubak-Turner/9781482210200/>
- Beier, C. M., Sink, S. E., Hennon, P. E., D'Amore, D. V., & Juday, G. P. (2008). Twentieth-century warming and the dendroclimatology of declining yellow-cedar forests in southeastern Alaska. *Canadian Journal of Forest Research*, *38*(6), 1319-1334.
- Besag, J. (1977). Contribution to the discussion of Dr. Ripley's paper. *JR Stat. Soc. B*, *39*(2), 193-195.
- Brown, J. H., Stevens, G. C., & Kaufman, D. M. (1996). The geographic range: size, shape, boundaries, and internal structure. *Annual review of ecology and systematics*, 597-623.
- Buma, B., Hennon, P. E., Bidlack, A. L., Baichtal, J. F., Ager, T. A., & Streveler, G. (2014). Correspondence regarding "The problem of conifer species migration lag in the Pacific Northwest region since the last glaciation" by Elias, S.A., (2013), *Quaternary Science Reviews* *77*, 55–69. *Quaternary Science Reviews*. In press.
- Buma, B., & Barrett, T. M. (2015). Spatial and topographic trends in forest expansion and biomass change, from regional to local scales. *Global change biology*, *21*(9), 3445-3454.
- Buma, B., Hennon, P.E., Harrington, C.A., Popkin, J.R., Krapek, J., Lamb, M.S, Oakes, L.E., Saunders, S., & Zeglen, S. (2016). Emerging climate-driven disturbance processes: widespread mortality associated with snow-to-rain transitions across 10° of latitude and half the range of a climate-threatened conifer. *Global change Biology*. In press.
- Burns, R. M., & Honkala, B. H. (1990). Silvics of North America. Volume 1. Conifers. *Agriculture Handbook (Washington)*, (654).
- Cheddadi, R., Vendramin, G. G., Litt, T., François, L., Kageyama, M., Lorentz, S., Laurent, J. M., DeBeaulieu, J. L., Sardori, L., Jost, A., & Lunt, D. (2006). Imprints of glacial refugia in the modern genetic diversity of *Pinus sylvestris*. *Global Ecology and Biogeography*, *15*(3), 271-282.

- Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333(6045), 1024-1026.
- D'Amore, D. V., Hennon, P. E., Schaberg, P. G., & Hawley, G. J. (2009). Adaptation to exploit nitrate in surface soils predisposes yellow-cedar to climate-induced decline while enhancing the survival of western redcedar: A new hypothesis. *Forest Ecology and Management*, 258(10), 2261-2268.
- Davis, A. J., Jenkinson, L. S., Lawton, J. H., Shorrocks, B., & Wood, S. (1998). Making mistakes when predicting shifts in species range in response to global warming. *Nature*, 391(6669), 783-786.
- Davis, M. A., Grime, J. P., & Thompson, K. (2000). Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, 88(3), 528-534.
- Davis, M. B., & Shaw, R. G. (2001). Range shifts and adaptive responses to Quaternary climate change. *Science*, 292(5517), 673-679.
- Deal, R. L., Oliver, C. D., & Bormann, B. T. (1991). Reconstruction of mixed hemlock-spruce stands in coastal southeast Alaska. *Canadian Journal of Forest Research*, 21(5), 643-654.
- DeMeo, T., Martin, J., & West, R. A. (1992). *Forest plant association management guide: Ketchikan area, Tongass National Forest*. US Forest Service, Tongass National Forest, Ketchikan Area.
- Diniz-Filho, J. A. F., Bini, L. M., & Hawkins, B. A. (2003). Spatial autocorrelation and red herrings in geographical ecology. *Global ecology and Biogeography*, 12(1), 53-64.
- Dubois, G., & Burr, S. (2015). FS-R10-FHP. Forest Health Conditions in Alaska 2015. Anchorage, Alaska. U.S. Forest Service, Alaska Region. Publication R10-PR-38. 78 Pages
- Ellenwood, J. R., Krist, F. J., & Romero, S. A. (2015). National Individual Tree Species Atlas. *United States Department of Agriculture, Forest Service, Fort Collins, CO. Available at: [http://www.fs.fed.us/foresthealth/technology/pdfs/FHTET\\_15\\_01\\_National\\_Individual\\_Tree\\_Species\\_Atlas\\_Spread.pdf](http://www.fs.fed.us/foresthealth/technology/pdfs/FHTET_15_01_National_Individual_Tree_Species_Atlas_Spread.pdf).*
- Fajardo, A., Goodburn, J. M., & Graham, J. (2006). Spatial patterns of regeneration in managed uneven-aged ponderosa pine/Douglas-fir forests of Western Montana, USA. *Forest Ecology and Management*, 223(1), 255-266.
- Gessler, P. E., Moore, I. D., McKenzie, N. J., & Ryan, P. J. (1995). Soil-landscape modelling and spatial prediction of soil attributes. *International Journal of Geographical Information Systems*, 9(4), 421-432.
- Hansen, B. C., & Engstrom, D. R. (1996). Vegetation history of Pleasant Island, southeastern Alaska, since 13,000 yr BP. *Quaternary Research*, 46(2), 161-175.

- Harris, A. S., Hutchison, K., Meehan, W. R., Swanston, D. N., Helmers, A. E., Hendee, J. C., & Collins, T. M. (1974). The forest ecosystem of southeast Alaska: 1. The setting. Gen. Tech. Rep. PNW-GTR-012. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 46 p.
- Hawkins, B. J., Russell, J., & Shortt, R. (1994). Effect of population, environment, and maturation on the frost hardiness of yellow-cedar (*Chamaecyparis nootkatensis*). *Canadian Journal of Forest Research*, 24(5), 945-953.
- Hennon, P. E., Shaw, C. G., & Hansen, E. M. (1990). Dating decline and mortality of *Chamaecyparis nootkatensis* in southeast Alaska. *Forest Science*, 36(3), 502-515.
- Hennon, P. E. (1992). *Current knowledge of ecology and silviculture of yellow-cedar in southeast Alaska: information exchanged at Sitka, Alaska, November 1991*. Alaska Region, USDA Forest Service.
- Hennon, P. E., D'Amore, D. V., Schaberg, P. G., Wittwer, D. T., & Shanley, C. S. (2012). Shifting climate, altered niche, and a dynamic conservation strategy for yellow-cedar in the North Pacific coastal rainforest. *BioScience*, 62(2), 147-158.
- Hennon, P. E., McKenzie, C. M., D'Amore, D., Wittwer, D. T., Mulvey, R. L., Lamb, M. S., Biles, F. E., & Cronn, R. C. (2016). A climate adaptation strategy for conservation and management of yellow-cedar in Alaska. PNW-GTR-917. US Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Heusser, C. J., Heusser, L. E., & Peteet, D. M. (1985). Late-Quaternary climatic change on the American North Pacific coast. *Nature*, 315(6019), 485-487.
- Ibáñez, I., Clark, J. S., & Dietze, M. C. (2009). Estimating colonization potential of migrant tree species. *Global Change Biology*, 15(5), 1173-1188.
- Krapek, J., & Buma, B. (2015). Yellow-cedar: climate change and natural history at odds. *Frontiers in Ecology and the Environment*, 13(5), 280-281.
- Krapek, J., Hennon, P.E., D'Amore, D.V., & Buma, B. Despite available habitat, migration of climate-threatened tree appears punctuated with last pulse during the Little Ice Age climate period. Prepared for submission in the Journal of Biogeography.
- Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, 462(7276), 1052-1055.
- Lazarus, E. D., & McGill, B. J. (2014). Pushing the pace of tree species migration. *PloS one*, 9(8), e105380.

- Lertzman, K. P. (1995). Forest dynamics, differential mortality and variable recruitment probabilities. *Journal of Vegetation Science*, 6(2), 191-204.
- Lindsay, C., Zhu, J., Miller, A. E., Kirchner, P., & Wilson, T. L. (2015). Deriving Snow Cover Metrics for Alaska from MODIS. *Remote Sensing*, 7(10), 12961-12985. Snow cover metrics available at: <http://www.gina.alaska.edu/projects/modis-derived-snow-metrics>
- Mann, D. H. (1986). Wisconsin and Holocene glaciation of southeast Alaska. Glaciation in Alaska: The Geologic Record. *Alaska Geological Society*. Pages 237-265
- Martin, J.R., Trull, S.J., Brady, W.W., West, R.A., & Downs, J.M. (1995). Forest Plant Association Management Guide: Chatham Area Tongass National Forest. R10-TP-57. USDA Forest Service, Juneau, AK.
- McLachlan, J. S., Clark, J. S., & Manos, P. S. (2005). Molecular indicators of tree migration capacity under rapid climate change. *Ecology*, 86(8), 2088-2098.
- Moeur, M. (1993). Characterizing spatial patterns of trees using stem-mapped data. *Forest science*, 39(4), 756-775.
- Morin, X., & Thuiller, W. (2009). Comparing niche-and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology*, 90(5), 1301-1313.
- Ott, R. A., & Juday, G. P. (2002). Canopy gap characteristics and their implications for management in the temperate rainforests of southeast Alaska. *Forest Ecology and Management*, 159(3), 271-291.
- Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918), 37-42.
- Pawuk, W. H., & Kissinger, E. J. (1989). Preliminary forest plant associations of the Stikine area, Tongass National Forest. *USDA Forest Service, Technical Publication R10-TP-72*.
- Pearson, R. G., & Dawson, T. P. (2005). Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change. *Biological Conservation*, 123(3), 389-401.
- Petit, R. J., Hu, F. S., & Dick, C. W. (2008). Forests of the past: a window to future changes. *Science*, 320(5882), 1450-1452.
- Peteet, D.M. (2000). Sensitivity and rapidity of vegetational response to abrupt climate change. *Proceedings of the National Academy of Sciences*, 97(4), 1359-1361.
- Ripley, B. D. (1977). Modelling spatial patterns. *Journal of the Royal Statistical Society. Series B (Methodological)*, 172-212.
- Russell, J., Grossnickle, S. C., Ferguson, C., & Carson, D. W. (1990). Yellow-cedar stecklings: nursery production and field performance.

- Schaberg, P. G., Hennon, P. E., D'Amore, D. V., & Hawley, G. J. (2008). Influence of simulated snow cover on the cold tolerance and freezing injury of yellow-cedar seedlings. *Global Change Biology*, *14*(6), 1282-1293.
- Sexton, J. P., McIntyre, P. J., Angert, A. L., & Rice, K. J. (2009). Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 415-436.
- USGS (2015). Alaska IFSAR Digital Elevation Model. Available at: <http://ifsar.gina.alaska.edu/>
- Van der Knaap, W. O., van Leeuwen, J. F., Finsinger, W., Gobet, E., Pini, R., Schweizer, A., Valsecchi, V. & Ammann, B. (2005). Migration and population expansion of *Abies*, *Fagus*, *Picea*, and *Quercus* since 15000 years in and across the Alps, based on pollen-percentage threshold values. *Quaternary Science Reviews*, *24*(5), 645-680.
- Walck, J. L., Hidayati, S. N., Dixon, K. W., Thompson, K. E. N., & Poschlod, P. (2011). Climate change and plant regeneration from seed. *Global Change Biology*, *17*(6), 2145-2161.
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., Fromentin, J. M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, *416*(6879), 389-395.
- Wiles, G. C., D'Arrigo, R., Barclay, D., Wilson, R. S., Jarvis, S. K., Vargo, L., & Frank, D. (2014). Surface air temperature variability reconstructed with tree rings for the Gulf of Alaska over the past 1200 years. *The Holocene*, *40*(2), 198-208.
- Williams, J. W., Post, D. M., Cwynar, L. C., Lotter, A. F., & Levesque, A. J. (2002). Rapid and widespread vegetation responses to past climate change in the North Atlantic region. *Geology*, *30*(11), 971-974.
- Zhu, K., Woodall, C. W., & Clark, J. S. (2012). Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology*, *18*(3), 1042-1052.

## General Conclusions

This is the first study to examine yellow-cedar's recent migration history and present day expansion at the species' leading northeastern range edge. Characterizing yellow-cedar's migration and future dispersal capacity in an era of rapid climate change is critical for many reasons. First, yellow-cedar is a regionally important tree, with high economic and cultural value, that fills a unique niche on the landscape. Therefore, predicting where this tree will succeed and potentially migrate in future climates is of considerable interest to forest users, managers, and conservationists alike. Second, yellow-cedar is dying on large portions of the landscape farther south in its range, only ~100 km south of the populations identified in this study. Understanding the adaptive capacity of yellow-cedar to keep its leading edge ahead of its trailing edge is a leading conservation concern (Hennon et al. 2016). Finally, yellow-cedar could serve as an example for other long-lived, but dispersal-limited, tree species that will have to adapt to uncertain climate futures as they must disperse through intact forests to track climate.

By mapping 11 range edge yellow-cedar populations near Juneau, Alaska, estimating population establishment ages, and quantifying current occupancy of suitable habitat in the study area, we support current hypotheses about yellow-cedar's ongoing natural migration in the region (Hennon et al. 2012, Buma et al. 2014). Yellow-cedar populations in the study area appear to have established and spread to their current extent during the Little Ice Age climate period (1100 – 1850, Wiles et al. 2014), generally on north facing, protected slopes, but populations are currently occupying less than one percent of yellow-cedar's potential landscape niche near the Juneau area.

Despite abundant unoccupied habitat, and evidence of ongoing yellow-cedar migration, stand expansion appears limited in the study area, with few seedlings surviving to maturity outside of existing stand boundaries. Additionally, large, ~100 -200-year-old trees are located abruptly at existing population edges, indicating that stand expansion has been limited since the end of the Little Ice Age. Other regional yellow-cedar studies have noted that most mature yellow-cedar trees in southeast Alaska regenerated and grew to canopy status during the Little Ice Age (Hennon et al. 1990, Beier et al. 2008) and that yellow-cedar regeneration via seed is currently limited, particularly in closed canopy forests (Pawuk and Kissinger 1989, DeMeo et al. 1992, Martin et al. 1995, Hennon et al. 2016). Seedling germination and success, where observed, support yellow-cedar's previously identified niche in the region of moderately wet, higher light (i.e., open canopy) forests (Harris et al. 1974, Martin et al. 1995, Hennon et al. 2016).

Although stand expansion and yellow-cedar regeneration via seed is currently limited, vegetative regeneration is abundant across populations in our study. Vegetative regeneration may be an



adaptive strategy that allows this long-lived species to persist on the landscape in periods that are unfavorable for sexual reproduction, but is not a strategy for mid to long term dispersal. Yellow-cedar migration history in the region appears punctuated, with a last pulse of successful sexual reproduction and colonization during the Little Ice Age climate period, indicating that this strategy may be successful in the long term. Long-lived species like yellow-cedar are “stress tolerators” (Antos et al. 2016) and their longevity allows for persistence on the landscape, even when recruitment is unfavorable in the short term (Lertzman 1995).

Species range shifts are often episodic during periods of abrupt climate change (Walther et al. 2002), and yellow-cedar appears to be an example of a species that undergoes pulsed migration and expansion when climate and/or forest conditions are favorable. Wind dispersed trees, like yellow-cedar, are capable of rapid rates of migration (Lazarus and McGill 2014) when optimal conditions exist. Preliminary molecular DNA work from yellow-cedar foliage collections across its range suggest that Alaska populations were founded by diverse sources and “expanded at an exponential rate” at some point in the past, perhaps during the Little Ice Age (Cronn et al. 2014, Hennon et al. 2016). With a return to cooler and snowier conditions at some point in the future, yellow-cedar could go through another pulse of successful regeneration to colonize available habitat; however this currently appears unlikely given projected future climate scenarios (Hennon et al. 2016).

Yellow-cedar’s currently limited dispersal capacity and lack of stand expansion in recent decades should be considered when planning for the future management and conservation of this high value tree in Alaska. Preservation in areas that will remain snowy and assisted migration to suitable habitats (i.e., snowy, moderately wet, open canopy) are warranted management considerations for yellow-cedar (Lazarus and McGill 2014, Hennon et al. 2016). With yellow-cedar’s trailing edge approaching its leading edge in southeast Alaska, these factors are particularly important to consider.

In the context of yellow-cedar’s entire range, it appears that the species will remain healthy in drastically reduced, yet substantial, areas on the landscape over the next century that remain snowy enough to protect yellow-cedar roots (Hennon et al. 2016, Buma et al. 2016). As a “climate generalist” that has persisted on the landscape for millions of years through diverse environmental conditions, the species will likely occupy a distinct, if reduced, niche on the landscape even in uncertain future climate scenarios (Hennon et al. 2016). However, current projections of climate-induced mortality will drastically reduce the area of yellow-cedar on the landscape, and currently limited migration and expansion north and upwards in elevation are unlikely to make up for these losses. In that context,

forest managers should consider if preservation and assisted migration strategies are warranted to maintain the current proportional occupancy of the landscape by this high value tree.

## General References

- Antos, J. A., Filipescu, C. N., & Negrave, R. W. (2016). Ecology of western redcedar (*Thuja plicata*): Implications for management of a high-value multiple-use resource. *Forest Ecology and Management*, 375, 211-222.
- Beier, C. M., Sink, S. E., Hennon, P. E., D'Amore, D. V., & Juday, G. P. (2008). Twentieth-century warming and the dendroclimatology of declining yellow-cedar forests in southeastern Alaska. *Canadian Journal of Forest Research*, 38(6), 1319-1334.
- Buma, B., Hennon, P. E., Bidlack, A. L., Baichtal, J. F., Ager, T. A., & Streveler, G. (2014). Correspondence regarding "The problem of conifer species migration lag in the Pacific Northwest region since the last glaciation" by Elias, S.A., (2013), *Quaternary Science Reviews* 77, 55–69. *Quaternary Science Reviews*. In press.
- Buma, B., Hennon, P.E., Harrington, C.A., Popkin, J.R., Krapek, J., Lamb, M.S, Oakes, L.E., Saunders, S., & Zeglen, S. (2016). Emerging climate-driven disturbance processes: widespread mortality associated with snow-to-rain transitions across 10° of latitude and half the range of a climate-threatened conifer. *Global change Biology*. In press.
- Carrara, P. E., Ager, T. A., & Baichtal, J. F. (2007). Possible refugia in the Alexander Archipelago of southeastern Alaska during the late Wisconsin glaciation. *Canadian Journal of Earth Sciences*, 44(2), 229-244.
- Cronn, R. C., Jennings, T. N., Hennon, P. E., & D'Amore, D. V. (2014). Development of DNA tools to aid genetic conservation and restoration in Alaska yellow-cedar. Final report, U.S. Forest Service Special Technology Development program. Fairbanks, AK: U.S. Department of Agriculture, Forest Service, Alaska Forest Health and Protection Office. 64 p.
- Davis, M. B., & Shaw, R. G. (2001). Range shifts and adaptive responses to Quaternary climate change. *Science*, 292(5517), 673-679.
- DeMeo, T., Martin, J., & West, R. A. (1992). *Forest plant association management guide: Ketchikan area, Tongass National Forest*. US Forest Service, Tongass National Forest, Ketchikan Area.
- Dubois, G. & Burr, S. (2015). FS-R10-FHP. Forest Health Conditions in Alaska 2015. Anchorage, Alaska. U.S. Forest Service, Alaska Region. Publication R10-PR-38. 78 p.
- Harris, A. S., Hutchison, K., Meehan, W. R., Swanston, D. N., Helmers, A. E., Hendee, J. C., & Collins, T. M. (1974). The forest ecosystem of southeast Alaska: 1. The setting. Gen. Tech. Rep. PNW-GTR-012. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 46 p.
- Hennon, P. E., Shaw, C. G., & Hansen, E. M. (1990). Dating decline and mortality of *Chamaecyparis nootkatensis* in southeast Alaska. *Forest Science*, 36(3), 502-515.

- Hennon, P. E., D'Amore, D. V., Schaberg, P. G., Wittwer, D. T., & Shanley, C. S. (2012). Shifting climate, altered niche, and a dynamic conservation strategy for yellow-cedar in the North Pacific coastal rainforest. *BioScience*, *62*(2), 147-158.
- Hennon, P. E., McKenzie, C. M., D'Amore, D., Wittwer, D. T., Mulvey, R. L., Lamb, M. S., Biles, F. E., & Cronn, R. C. (2016). A climate adaptation strategy for conservation and management of yellow-cedar in Alaska. PNW-GTR-917. US Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Hille Ris Lambers, J., Anderegg, L. D., Breckheimer, I., Burns, K. M., Ettinger, A. K., Franklin, J. F., Freund, J. A., Ford, K.R., & Krolss, S. J. (2015). Implications of Climate Change for Turnover in Forest Composition. *Northwest Science*, *89*(3), 201-218.
- Lazarus, E. D., & McGill, B. J. (2014). Pushing the pace of tree species migration. *PloS one*, *9*(8), e105380.
- Lertzman, K. P. (1995). Forest dynamics, differential mortality and variable recruitment probabilities. *Journal of Vegetation Science*, *6*(2), 191-204.
- Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, *462*(7276), 1052-1055.
- Malcolm, J. R., Markham, A., Neilson, R. P., & Garaci, M. (2002). Estimated migration rates under scenarios of global climate change. *Journal of Biogeography*, *29*(7), 835-849.
- Martin, J.R., Trull, S.J., Brady, W.W., West, R.A., & Downs, J.M. (1995). Forest Plant Association Management Guide: Chatham Area Tongass National Forest. R10-TP-57. USDA Forest Service, Juneau, AK.
- Pawuk, W. H., & Kissinger, E. J. (1989). Preliminary forest plant associations of the Stikine area, Tongass National Forest. *USDA Forest Service, Technical Publication R10-TP-72*.
- Schaberg, P. G., D'Amore, D. V., Hennon, P. E., Halman, J. M., & Hawley, G. J. (2011). Do limited cold tolerance and shallow depth of roots contribute to yellow-cedar decline?. *Forest Ecology and Management*, *262*(12), 2142-2150.
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., Fromenthin, J. M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, *416*(6879), 389-395.
- Wiles, G. C., D'Arrigo, R., Barclay, D., Wilson, R. S., Jarvis, S. K., Vargo, L., & Frank, D. (2014). Surface air temperature variability reconstructed with tree rings for the Gulf of Alaska over the past 1200 years. *The Holocene*, *40*(2), 198-208.