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Limited stand expansion by a long-lived conifer at a leading northern range edge, despite available habitat

John Krapek[1] 🆔 | Brian Buma[2] 🆔

[1]School of Natural Resources and Extension, University of Alaska Fairbanks, Fairbanks, AK, USA

[2]Department of Natural Sciences, University of Alaska Southeast, Juneau, AK, USA

Correspondence
John Krapek
Email: jpkrapek@alaska.edu

Present address
John Krapek, Department of Natural Sciences, University of Alaska Southeast, Juneau, AK, USA

Abstract

1. In an era of rapid climate change, understanding the natural capacity of species' ranges to track shifting climatic niches is a critical research and conservation need. Because species do not move across the landscape through empty space, but instead have to migrate through existing biotic communities, basic dispersal ecology and biotic interactions are important considerations beyond simple climate niche tracking.

2. Yellow-cedar (*Callitropsis nootkatensis*), 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. At the same time, yellow-cedar's trailing edge is approaching its leading edge in the region, due to climate-induced root injury leading to widespread mortality over the past century. To examine the current dispersal capacity of yellow-cedar at its leading range edge, and potential for the species' leading edge to stay ahead of its trailing edge, we characterized recent yellow-cedar stand development near Juneau, Alaska, and surveyed the spread of yellow-cedar seedlings just beyond existing stand boundaries.

3. Despite suitable habitat beyond stand edges, stand expansion appears limited in recent decades to centuries. Large quantities of seed are germinating within stands and just beyond boundaries, but seedlings are not developing to maturity. Furthermore, *c.* 100–200-year-old yellow-cedar trees are located abruptly at stand boundaries, indicating stand expansion is in a period of stasis with a last pulse at the end of the Little Ice Age climate period.

4. 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 favourable for successful seedling recruitment, leading to an overall punctuated migration and colonization of new landscapes.

5. *Synthesis.* Species ranges do not always respond linearly to shifting climatic conditions. Instead, successful colonization of new habitat may be tied to episodic, threshold-related landscape phenomena, dispersal ability, and competition with existing plant communities.

KEYWORDS
biotic interactions, *Callitropsis nootkatensis*, climate change, competition, dispersal, persistence niche, punctuated range extension, range shift, yellow-cedar

1 | INTRODUCTION

Species' ranges are in constant flux as they track ever-shifting biotic and abiotic niches on the landscape through time (Brown, Stevens, & Kaufman, 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 range expansions, contractions and movements for future landscape biodiversity and ecosystem services (Sax, Early, & Bellemare, 2013; Sexton, McIntyre, Angert, & Rice, 2009). Considerable work in recent years has focused on exploring how current species distributions have shifted in recent decades at leading and trailing range edges (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Scheele, Foster, Banks, & Lindenmayer, 2017; Zhu, Woodall, & Clark, 2012) and modelling how species may continue to move as they respond to ameliorating or worsening abiotic conditions (Morin & Thuiller, 2009). Biogeographers have examined past range shifts through extensive exploration of the fossil record (Peteet, 2000; Van der 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, Clark, & Manos, 2005; Petit, Hu, & Dick, 2008).

There are two broad conceptual models of species shifts: gradual expansion vs. punctuated expansion. Gradual expansion is driven by generational time in a generally favourable climate, where local dispersal dominates (Chen et al., 2011), while punctuated expansion exhibits extended periods of relative stasis that are periodically interrupted by long-distance dispersal and establishment (Davis & Shaw, 2001; Jackson, Betancourt, Booth, & Gray, 2009). The two models have important implications for species' adaptability to climate change, as the former implies predictability while the second suggests a more stochastic process. Realized species distributions are theorized to be constrained by four processes: abiotic conditions, biotic interactions, dispersal limitations and the evolutionary capacity of a population to adapt to new environments (Soberon & Peterson, 2005). In terms of range expansion, relaxation of those four constraints, or the most limiting, should then correspond to expansion in either a punctuated (stepped relaxation) or a gradual (a general smooth amelioration of harsh conditions) manner. While ranges are always in flux due to historical climate shifts, the rapidity and directionality of anthropogenic climate change lends urgency to better understanding the dynamics of range shifts (Davis & Shaw, 2001; Loarie et al., 2009).

Although a rapidly changing climate will exert a significant influence on species range shifts through changing top-down abiotic drivers (shifts in the climatic envelope of a given species), basic dispersal dynamics and biotic factors are key controls on range movements (Jackson et al., 2009; Soberon & Peterson, 2005). Inter- and intraspecific 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 (Pearson & Dawson, 2005; Walck, Hidayati, Dixon, Thompson, & Poschlod, 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 new habitats (Ibáñez, Clark, & Dietze, 2009; Walck et al., 2011) and the potential for the establishment of self-sustaining populations, non-sink populations (Pulliam, 1988). Studying the fine-scaled spatial patterns of plant recruitment at a current leading or trailing range edge can answer questions about competition and dispersal ability in the context of where changing climate may also have the largest influence on shifting niches.

Yellow-cedar (*Callitropsis nootkatensis* D. Don; Oerst. ex D.P. Little [alternatively *C. nootkatensis* D. Don]), a long-lived conifer of the North Pacific Coastal Temperate Rainforest (PCTR) region, is a well-documented example of a species undergoing a rapid change in the distribution of its suitable climate envelope (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 (Figure 1; Buma et al., 2014; Hennon, D'Amore, Schaberg, Wittwer, & Shanley, 2012), 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, Hennon, D'Amore, & Buma, 2017). At the same time, recent climate-driven mass mortality (termed "yellow-cedar decline") in warmer portions of its range, only *c.* 100 km south of its current contiguous northern range edge (Buma et al., 2016; Dubois & Burr, 2015; Hennon et al., 2012), is raising concerns about the viability of the species in a warmer climate.

Yellow-cedar appears to have large areas of potential habitat north of its current range edge, feasible for continued migration (Figure 2; Hennon et al., 2016; Krapek et al., 2017; Martin, Trull, Brady, West, & Downs, 1995). Despite yellow-cedar populations being present at the northern range edge for >675 years and establishing across a wide range of topo-edaphic conditions, the species has only occupied a small proportion of potential habitat along the range edge (Krapek et al., 2017). 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, herbivore species, plant community composition (Martin et al., 1995) and disturbance regime (Buma & Barrett, 2015), with the lack of yellow-cedar being the only substantive difference. Disjunct yellow-cedar populations in Prince William Sound, Alaska, approximately 500 km northwest of yellow-cedar's current contiguous range edge, are healthy and regenerating well despite growing in a cooler climate (Hennon & Trummer, 2001). Transplant experiments outside of the range are similarly growing well, and there is little genetic differentiation across the natural distribution of yellow-cedar, despite a span of over 20 degrees of latitude (Cronn, Jennings, Hennon, & D'Amore, 2014; Ritland, Pape, & Ritland, 2001). All these pieces of evidence suggest that the current distribution is driven by biotic interactions and/or dispersal limitations, as opposed to abiotic or genetic constraints.

In short, yellow-cedar appears to be an excellent case study for exploring the mechanisms and constraints on range expansion in a warming climate as plant community, climate, edaphic and disturbance conditions all appear to be non-limiting. The goal of this study was to examine isolated, leading edge yellow-cedar stands nested within large areas of suitable habitat and determine the rate and mechanisms

FIGURE 1 Yellow-cedar stands in study area near Juneau, Alaska. Map inset shows study area location in context of yellow-cedar's range. The modelled range (see Buma et al., 2016), was clipped from the study area. A small buffer was added to each stand so it is visible at the scale of the full study area. Stand abbreviations are included next to each polygon. The eight stands 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**. A trial yellow-cedar planting established in 2010 in an open canopy, snow area is currently growing well (Hennon et al., 2016) [Colour figure can be viewed at wileyonlinelibrary.com]
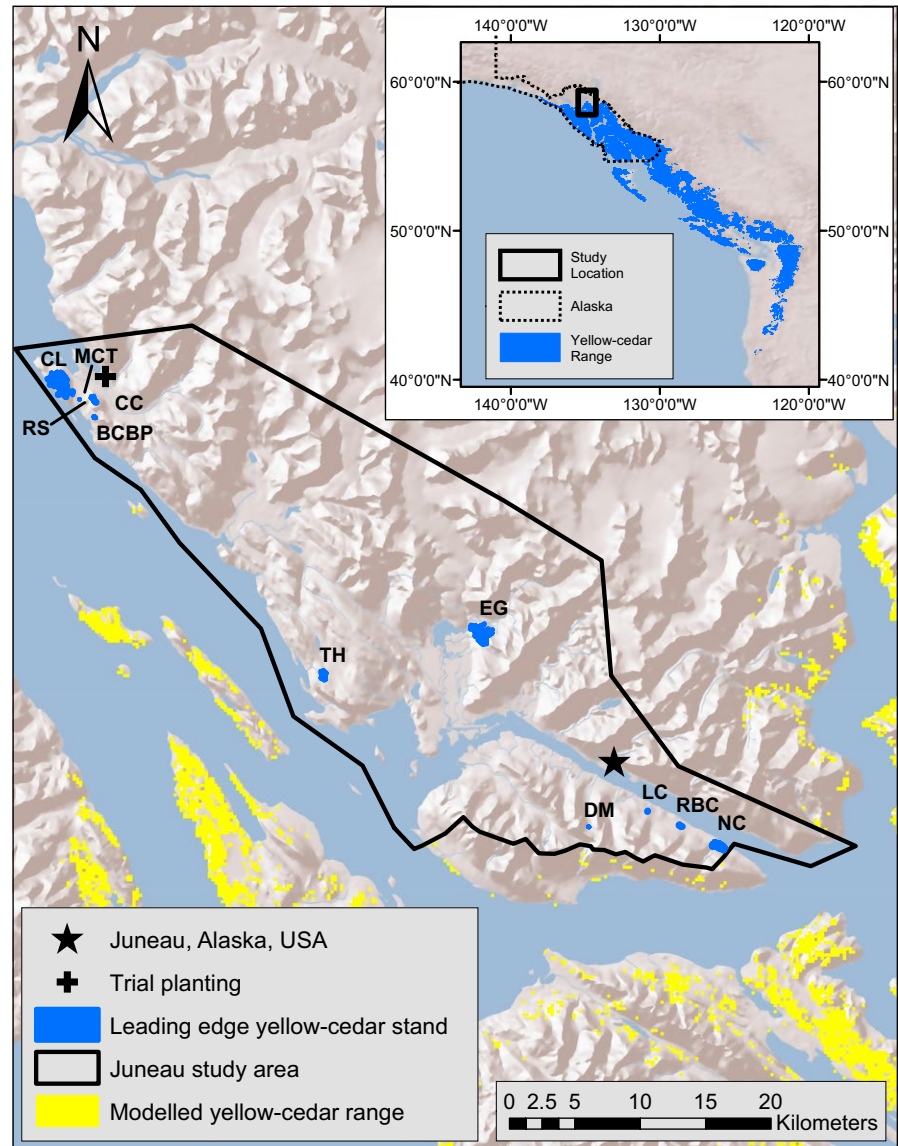
of population spread into neighbouring, undisturbed forests. We sought to answer the following questions:

1. Are range edge yellow-cedar stands successfully expanding into neighbouring forests? Is expansion gradual or punctuated?
2. Competition: Is yellow-cedar seedling establishment related to overstorey and understorey plant community composition?
3. Abiotic Factors: Is yellow-cedar seedling establishment related to abiotic factors (i.e., snow, soil drainage) known to be important for mature yellow-cedar trees?

2 | MATERIALS AND METHODS

2.1 | Study area description

The study area was located near Juneau, Alaska, USA (58°18′N, 134°25′W; 0 m to 1500 m a.s.l.), which lies just beyond yellow-cedar's

current contiguous northeast range edge (Figure 1). Yellow-cedar is rare in the surrounding forests, but there are large expanses of unoccupied, suitable habitat in the region (Krapek et al., 2017; Martin et al., 1995; Figure 2).

The climate in the study area is cool maritime with mean monthly temperatures ranging from −2 to 14°C at sea level throughout the year (NOAA, 2016), but significant variability at fine scales over steep topographic gradients. Precipitation is high, ranging from 1,000 to >5,000 mm annually with no summer drought period, leading to a landscape free of large fires and insect outbreaks (Martin et al., 1995) and a mosaic of late seral bog, shrubland and forest communities. The predominant forest disturbance in the region is localized wind-throw of trees, generally consisting of <1,000 m^2 patches with occasional stand replacing blowdown events and landslides (Buma & Barrett, 2015; Ott & Juday, 2002).

Tree diversity is low, with western hemlock (*Tsuga heterophylla* Raf., Sarg.) dominating most of the moderate to well-drained, undisturbed locations; mountain hemlock (*T. mertensiana* Bong., Carrière) replaces western hemlock in the subalpine zone and in some wetter
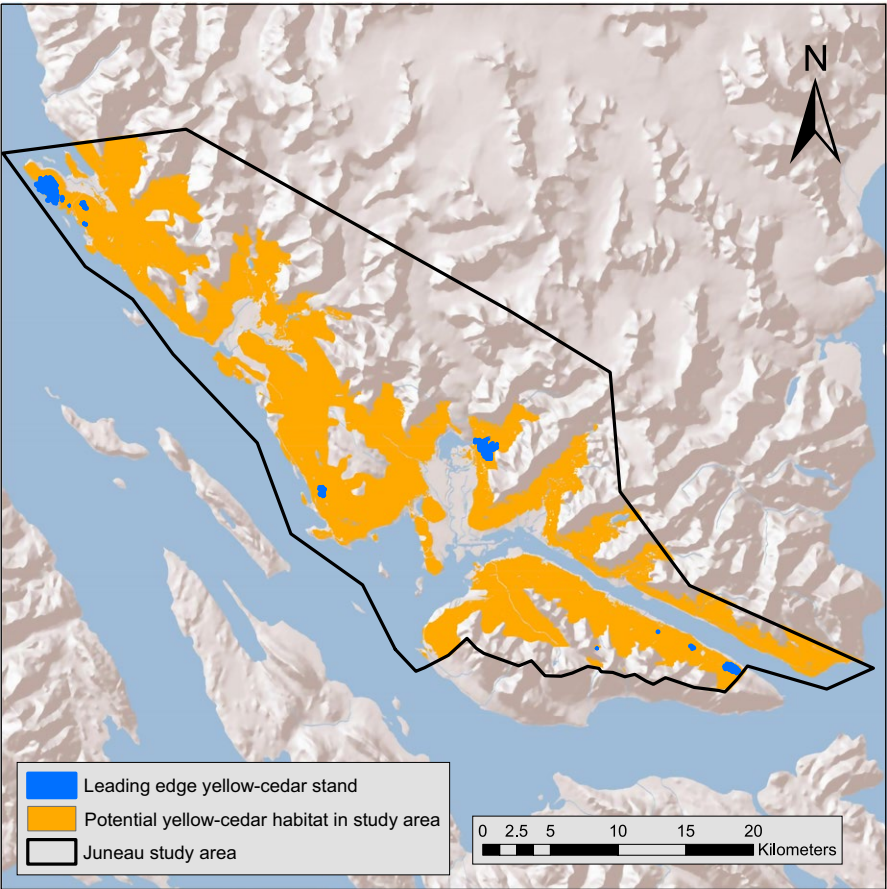
FIGURE 2 Potential yellow-cedar habitat in study area vs. locations yellow-cedar has colonized at the leading range edge. Potential habitat was modelled using topographic, climate and disturbance metrics common to where leading edge stands have established (Krapek et al., 2017). This modelling approach represents a high-end assumption of potential yellow-cedar habitat as it does not take into account biotic factors like seed dispersal ability or competition with other species. However, it generally illustrates that there are large portions of the landscape at the leading range edge that are potentially suitable for yellow-cedar growth if new establishment occurs. See Krapek et al. (2017) for full discussion of habitat modelling [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Information recorded for stem-mapped trees and yellow-cedar seedlings

Measurement	Units/notes
Trees (>1.4 m DBH)	
Species	*Callitropsis nootkatensis, Picea sitchensis, Tsuga heterophylla, Tsuga mertensiana*, unknown *Tsuga* sp., *Alnus rubra, Alnus viridis* ssp. *sinuata, Sorbus sitchensis, Malus fusca*
Understorey plant association	Dominant plant association in 3-m radius according to Martin et al. (1995)
Diameter at breast height (DBH)	Centimetres (cm)
Yellow-cedar regeneration (<1.4 DBH)	
Understorey 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	First year germinant or second year plus
Height of seedlings from seed[a]	Centimetres (cm)

[a]Heights measured on a subset of 10 plots.

community types (Martin et al., 1995). Sitka spruce (*Picea sitchensis* Bong., Carrière) is most competitive in areas of local disturbance (e.g., floodplains) where its fast growth on mineral soils is favoured. Patches of alder (*Alnus* spp.) and black cottonwood (*Populus balsamifera* L. ssp. *trichocarpa* [Torr. & A. Gray ex Hook.] Brayshaw) are also common in disturbed areas, while alders and willows (*Salix* spp.) dominate recently deglaciated areas and steep slopes.

2.2 | Yellow-cedar niche and ecology

Yellow-cedar, considered a climate generalist (Hennon et al., 2016) and "stress tolerator" (Antos, Filipescu, & Negrave, 2016), with a range spanning more than 20 degrees of latitude (Buma et al., 2016), grows in multiple forest types and possesses a wide-range of environmental tolerances. However, the species is most competitive within a

particular niche in southeast Alaska: moderately to marginally productive sites with poor drainage and/or shallow soils, such as the edges of bogs where its slow growth and decay resistance are favoured (Hennon et al., 2016). In wet landscapes, yellow-cedar is also uniquely adapted to take advantage of shallow sources of soil nitrogen unavailable to other plants, as the tree balances the metabolically taxing uptake of nitrate anions with excess calcium cation accumulation (D'Amore, Hennon, Schaberg, & Hawley, 2009). Because yellow-cedar is less shade-tolerant than western hemlock (Martin et al., 1995), it is more competitive in sites with open canopies, and can also become co-dominant where conditions (e.g., canopy gaps) allow for successful reproduction and recruitment in closed canopy forests.

Yellow-cedar reproduces sexually through seed and asexually through vegetative layering. Layering is particularly common in open canopy peatlands where lower limbs of trees are retained and can be separated from parent plants by organic matter accumulation (Hennon, Shaw, & Hansen, 1990). Layering is also common in areas where heavy snow (e.g., tree line) depresses branches. An insulating snowpack is important for protecting mature yellow-cedar tree roots from winter and spring freezing events (Hennon et al., 2012; Schaberg, Hennon, D'Amore, & Hawley, 2008). Insulating snow may also provide protection for fragile juvenile foliage (Hawkins, Russell, & Shortt, 1994; Russell, Grossnickle, Ferguson, & Carson, 1990), and likely protects seedlings from ungulate browse each winter (Hennon et al., 2016).

2.3 | Plot location at stand edges

The geographic extent of leading edge yellow-cedar stands in the Juneau study area was mapped in 2014–2015 (Figure 1), spanning a wide range of local topo-edaphic conditions (Krapek et al., 2017; data available from Dryad Digital Repository (https://doi.org/10.5061/dryad.7rd7s)) (Krapek & Buma, 2017). Edges of stands were delineated

based on the location of mature trees (≥1.4 m in height); any yellow-cedar regeneration (<1.4 m in height) located outside of the mature trees were considered separate from the yellow-cedar stand and represent expansion into non-yellow-cedar forests. Stands ranged from a 0.04 ha patch of nine canopy dominants to a 151 ha yellow-cedar forest, with a median size of 3.78 ha. Stands are healthy and relatively young for the species (mean age = 295 years; Krapek et al., 2017), as adults live 500–750 years, on average, and commonly reach ages over 1,000 years (Hennon et al., 2016). This suggests an ongoing, directional migration north at the range edge, and that stands have the capacity to expand locally.

At eight stands, we randomly located 300-m² plots (30 × 10 m) along the boundary of the stand to document yellow-cedar regeneration and expansion into existing forests (n = 29 total plots). Each plot spanned a stand boundary, with 150-m² (15 × 10 m) of the plot extending into the yellow-cedar stand and 150-m² (15 × 10 m) of the plot extending outside the yellow-cedar stand (Figure 3). At one of the eight yellow-cedar stands where three of the plots were located, the stand was so small in area (c. 400 m²), that the three interior subplots located there would have overlapped with each other. Therefore, the entire stand was treated as one larger interior subplot, leading to only 27 interior subplots total, and 29 exterior subplots. Plot data are available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.7rd7s) (Krapek & Buma, 2017).

Because we located multiple plots at each of the eight stands, we wanted to ensure that plots located at the same stand were spatially independent (i.e., not pseudoreplicated) in terms of seedling spread and expansion. Within stands, 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 & Honkala, 1990; Hennon et al., 2016). Moran's I, a measure of spatial autocorrelation (Griffith,
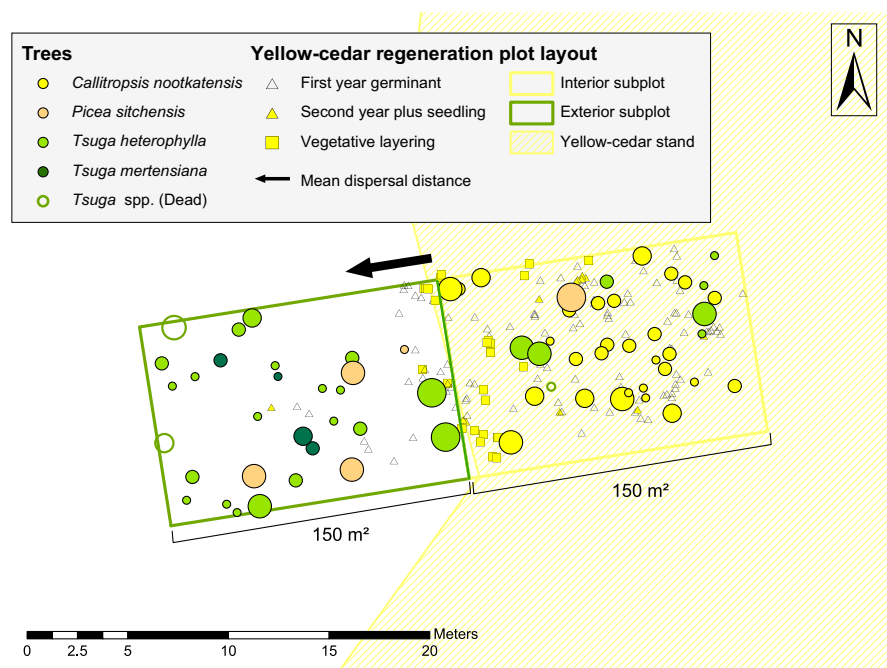

FIGURE 3 Stem map plot layout. Arrow represents the average seedling dispersal distance beyond edge of existing yellow-cedar stand for all 29 exterior subplots. Size of circle corresponds to diameter at breast height measurement for trees. This example plot is located at the Cedar Lake stand shown in Figure 1 [Colour figure can be viewed at wileyonlinelibrary.com]

1987), was used to compare seedling density values across plots with a spatially weighted matrix of between plot distances, and found to be insignificant (data not shown) (Diniz-Filho, Bini, & Hawkins, 2003). Therefore, we believe all plots were spatially independent in terms of seedling production and spread, the main focus of this study.

The locations of all trees (individuals >1.4 m diameter at breast height (DBH)) and yellow-cedar regeneration (individuals <1.4 m DBH) within plots were mapped (Figure 3) from a sub-metre accuracy GPS control point using a laser range finder with internal compass (TruPulse 360°R, Laser Technology, Inc., CO, USA). 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 sub-surface 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 "germi-nants" while seedlings surviving past the germinant stage are considered "second year plus" seedlings (Table 1).

Seedling heights were measured at 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. Similar to overall seedling counts described above, 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.

2.4 | Stand development

Three stands were fully stem-mapped (every tree; tree defined as individual >1.4 m DBH) to characterize stand development and canopy association with other species. Full stand maps allowed us to determine if small yellow-cedar trees were located at expanding edges of a stand, while larger individuals were located at the centre, or some point of initial establishment. We constructed density plots of overstorey yellow-cedar tree diameters in the stand edge subplots and the three fully stem mapped stands to compare size distributions.

Increment cores were taken from the largest yellow-cedar tree observed in 25 out of 27 interior subplots to determine an approximate

age of mature trees located at stand edges. Cores were prepared and aged using standard methods (Stokes & Smiley, 1968). Ages reported are minimum estimates: corrections were not applied to tree cores for height from base of tree, or rings missed due to internal decay due to a lack of published correction factors. Additionally, we targeted only the largest trees; large trees are often older, but not necessarily the oldest trees in each stand, as microsite and hydrology control size-growth patterns in the region (Buma, Krapek, & Edwards, 2016).

2.5 | Statistical analysis

2.5.1 | Seedling densities

We divided each 300 m^2 plot into its 150 m^2 "interior" and 150 m^2 "exterior" cedar stand components (Figure 3) for statistical analysis, leading to 56 subplots total. We calculated mean regeneration densities per hectare for germinants, second year plus seedlings by height class, and vegetative layering proportion, for interior and exterior subplots. For exterior subplots, we computed the mean, median and 95th percentile distance that seedlings dispersed beyond the stand edge. We used nonparametric Mann–Whitney U tests to determine if the probability of finding more seedlings of each height class was higher in interior or exterior subplots ($\alpha = 0.05$).

The most frequently observed understorey plant association in each subplot was assigned to the entire subplot to compare to regeneration densities by understorey plant cover. 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), to determine if seedling success varied along hydrologic gradients (Table 2).

To determine if seedling recruitment densities varied as a function of typical snowpack, we used the National Park Service and Geographic Information Network of Alaska 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, Zhu, Miller, Kirchner, & Wilson, 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 (Hennon et al., 2012). Some plots were located in the same snow pixel due to the coarse resolution of the dataset, even though microsite differences could be present. Regeneration densities were non-normally distributed along

TABLE 2 Observed understorey plant communities at yellow-cedar stands, ordered from dry to wet

Scientific name	*Vaccinium* spp. Type	*Vaccinium – Menziesia ferruginea*	*Cassiope* spp.	*Vaccinium – Nephrophyllidium crista-galli*	*Vaccinium – Lysichiton americanum*
Common name	blueberry type	Blueberry – False azalea	Mountain heather	Blueberry – deer cabbage	Blueberry – skunk cabbage
Percentage of poorly drained soils[a]	12	19	33	70	77

[a]Derived from Martin et al. (1995). When plant associations were combined (e.g., lumping upland blueberry type plant associations in the first column), the percentage of poorly drained soils was averaged.

the snow cover gradient, with increasing variance at higher snow cover values, so we used Spearman's rank correlation analysis to assess the relationship between snow and yellow-cedar regeneration.

2.5.2 | Point pattern analysis of yellow-cedar seedlings and overstorey trees

We used point pattern analysis to assess the spatial relationships between overstorey plant communities and yellow-cedar seedlings, and amongst yellow-cedar seedlings themselves, to determine if competition or facilitation might influence seedling success. Besag's $L(r)$ function (Besag, 1977) is a variance-stabilizing transformation of Ripley's $K(r)$ (Ripley, 1977), which improves interpretation of deviations in a point process from a hypothetical Poisson distribution at different distance lags (Baddeley, Rubak, & Turner, 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 spatial relationship). Additionally, we used the intertype $L_{1.2}(r)$ function, to examine bivariate spatial associations between yellow-cedar seedlings and the three dominant overstorey species (mountain hemlock, western hemlock and yellow-cedar) observed in plots (i.e., seedling to tree spatial relationship). We tested spatial associations at 1, 2, 3 and 4 m distance lags to avoid multiple comparisons of testing many lags, and reduce edge effects of larger lags because plots were only 10 m wide (Baddeley et al., 2015). We tested spatial associations for different trees in each subplot only if at least five trees of that species and five yellow-cedar seedlings were present to avoid point patterns with extremely low intensities. Vegetative regeneration was not considered in spatial tests due to its dependence on mature yellow-cedar.

Before implementing Besag's $L(r)$ function, we tested the point pattern in each subplot for complete spatial randomness (CSR), or adherence to a homogeneous Poisson process, following Baddeley et al. (2015). If a plot's point pattern was random ($p > .05$), we used a homogenous version of the $L(r)$ and intertype $L_{1.2}(r)$ functions, testing under assumptions of CSR. If the point pattern was not random ($p < .05$), indicating that the intensity of the point process varied through space, we fit a loglinear model to the data and tested under assumptions of inhomogeneous intensity. We generated a simulation envelope using 199 Monte Carlo runs for a null Poisson distribution to compare to the single observed point process, using isotropic edge correction. This led to 200 total evaluations of $L(r)$ at each lag, allowing us to compute p-values following methods from Baddeley et al. (2014); if observed $L(r)$ values at each lag were >195 simulated values, significant clustering was indicated ($p \leq .05$), while if observed values were <5 simulated values, significant inhibition ($p \leq .05$), or regularity in the point process, was indicated (Figure 4).

Because we tested spatial associations in many subplots, p-values for each spatial test at each lag were combined across all subplots using Fisher's combined probability test to control for the family wise error rate. Because we performed two-tailed spatial tests (clustering vs. inhibition at either tail), the combined Fisher statistic indicates if plots deviated from random association ($p < .05$), while the individual number of significant clustered or inhibited plots indicates tendency
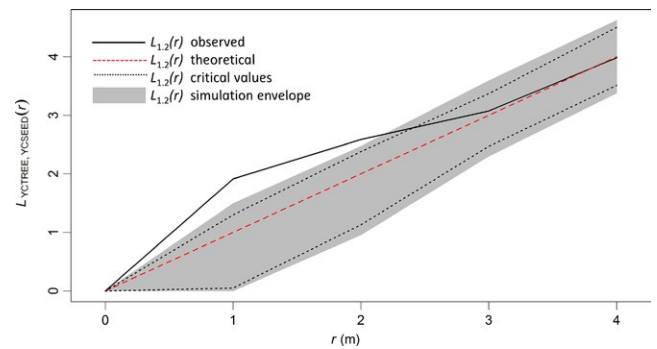

FIGURE 4 Example test of spatial association between yellow-cedar trees and yellow-cedar seedlings for one subplot. The observed $L_{1.2}(r)$ value for the subplot is the solid line, while the theoretical null Poisson model for a point pattern of this intensity is the long dashed line. The shaded area represents 199 simulations of complete spatial randomness. The short dashed lines are simulations near the upper and lower bounds of the simulation envelope, which represent the critical values for significant clustering or inhibition, according to methods from Baddeley et al. (2014). If the observed value at a particular lag lies above the upper critical value, significant clustering ($p \leq .05$) in the point pattern is indicated, while if it lies below the lower critical value, significant inhibition ($p \leq .05$) is supported [Colour figure can be viewed at wileyonlinelibrary.com]

towards clustering or inhibition. All computations were done using the *spatstat* (Baddeley et al., 2015) and *metap* (Dewey, 2017) packages in the R programming language.

3 | RESULTS

3.1 | Seedling maturation, seedling spread and incidence of vegetative regeneration

Yellow-cedar seedlings were observed in 21 of 29 exterior subplots, while seedlings were observed in all 27 interior subplots. Yellow-cedar germinants and second year plus seedlings were observed at significantly lower densities outside existing stand edges than inside stands ($p < .01$; Table 3). Yellow-cedar seedlings appear to follow standard rates of attrition for conifer species, with the most germinants per ha and fewer seedlings surviving into each successive life stage (Table 3). However, maturing seedlings (>10 cm in height) were uncommon in both interior ($M = 160$ per ha) and exterior ($M = 73$ per ha) subplots, with no significant difference in distributions between interior and exterior subplots ($p = .3$). 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 inside and outside stands ($p = 1.0$). Sub-tree size (100–140 cm) yellow-cedar seedlings were conspicuously absent from many plots and throughout stands as a whole (personal observation).

Vegetative regeneration, on the other hand, was widespread in interior subplots (1,698 individuals per ha) and predictably less common, but still prevalent, in exterior subplots (411 individuals

First year germinants # per ha		Second year plus seedlings # per ha		Maturing seedlings (10 cm+)[a] # per ha		Mature (100–140 cm) seedlings[a] # per ha		Vegetative regeneration (<1.4 m height) # per ha	
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)
2,178[b] ±1,850	765 ±1,165	**688** ±532	319 ±768	160 ±216	73 ±111	7 ±21	13 ±42	**1,698** ±1,778	411 ±659

[a]Seedling heights subsampled on only 10 plots.
[b]Bold indicates Mann–Whitney U significance (α = 0.05) of interior regeneration density exceeding that of exterior plot.

per ha). The difference in vegetative densities between interior and exterior subplots was significant ($p < .01$). Vegetative regeneration in exterior subplots occurred at the stand boundary, where mature yellow-cedar from inside the stand branched into the exterior plot (see Figure 3), or where maturing seedlings would branch underground.

On average, seedlings dispersed 4.65 m from stand boundaries into exterior subplots (see arrow on Figure 3). The median seedling dispersal distance was 4.08 m and the 95th percentile distance was 11.43 m. Of these dispersing seedlings, only 13 per hectare, or <1 per exterior subplot, survived to the 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 with the size of exterior subplots.

3.2 | Stand development and tree ages at stand boundaries

Diameter distributions of yellow-cedar trees 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, but many smaller saplings and pole-sized trees (Figure 5). The largest trees located in stand edge subplots were 191 years old on average (median = 199 years). The oldest tree observed in stand edge subplots 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 86 to 383-year-old (median = 199 years) yellow-cedar are present, indicating that stand boundaries have not moved more than 15 m since the early to late 1800s (approximate end of the Little Ice Age period; Wiles et al., 2014), on average.

3.3 | Point pattern analysis of yellow-cedar seedlings and overstorey trees

3.3.1 | Seedling to tree

Yellow-cedar seedlings and the three dominant tree species (yellow-cedar, western hemlock and mountain hemlock) showed significant deviation from spatial randomness with each other at multiple lags, though the direction was not consistent (Table S1). Overall, there
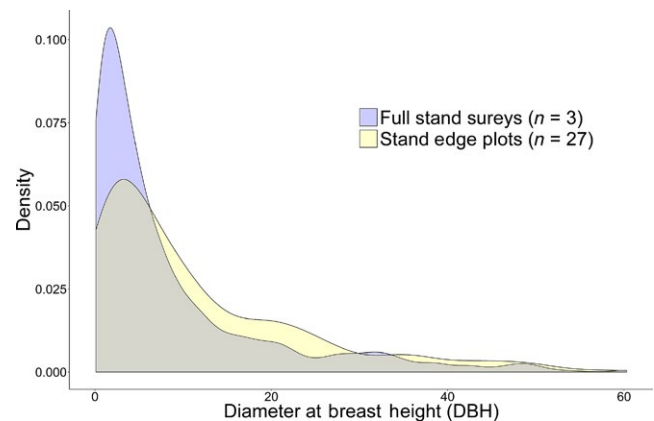

FIGURE 5 Pooled yellow-cedar tree (>1.4 m DBH) diameter distributions for 27 interior subplots and three fully stem-mapped yellow-cedar stands. Trees emanating from vegetative regeneration, when noted, were removed from histograms to reduce bias towards small individuals, as vegetative regeneration on 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" distribution, indicating old growth conditions [Colour figure can be viewed at wileyonlinelibrary.com]

were slightly more instances of inhibition between yellow-cedar seedlings and trees across subplots (Table S1), but many instances of non-significant association. In short, yellow-cedar seedlings show significant deviation from complete spatial randomness with trees across all subplots, with a slight tendency towards inhibition rather than clustering.

3.3.2 | Seedling to seedling

At the 1 m lag, yellow-cedar seedlings were significantly clustered in 15 subplots (Table 4, Fisher's combined $p < .001$). At the 2 m lag, seedlings showed significant deviation from spatial randomness across subplots (Fisher's combined $p < .01$) with significant clustering in four subplots, inhibition in one subplot and random spatial associations in the 29 remaining subplots. At 3 m lag distances, yellow-cedar seedlings showed marginally significant ($p = .05$) deviation from randomness across all plots, and there was no significant spatial association at the 4 m lag. In summary, seedlings were strongly clustered at short distances, with decreasing strength of clustering at increasing distance lags.

TABLE 4 Spatial relationships among yellow-cedar seedlings

|	Yellow-cedar seedling to seedling spatial association				
Lag (m)	Number of significant clustering	Number of significant inhibition	Number of non-significant	Total number of tests	Fisher's combined p
1	15	0	19	34	**<.001**
2	4	1	29	34	**<.01**
3	3	2	29	34	**.05**
4	3	2	29	34	.12

Bold indicates significance at α = 0.05.

3.4 | Yellow-cedar seedling densities in understorey plant communities

The highest seedling densities in interior (M = 3,433 per ha) and exterior (M = 1,615 per ha) subplots were observed in the blueberry—false azalea (*Vaccinium* spp.—*Menziesia ferruginea*) understorey plant association (Figure 6). Plots dominated by *Vaccinium* spp.—*Menziesia ferruginea* understorey communities also had the highest number of second year plus seedlings in both interior and exterior plots. Understorey plant communities dominated by blueberry and skunk cabbage (*Lysichiton americanum*) showed the second highest densities of yellow-cedar regeneration from seed in interior (M = 1,760 per ha) and exterior subplots (M = 278 per ha). Seedlings were less common in the mountain heather (*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 6).

FIGURE 6 Yellow-cedar regeneration densities in understorey 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 were lumped together. In one exterior plot, the dominant plant association was devil's club—skunk cabbage (*Oplopanax horridus—Lysichiton americanum*), and this plot was lumped with the blueberry—skunk cabbage (*Vaccinium* spp. —*L. americanum*) category due to similar composition and soil drainage. The number of subplots falling in each community type is listed in parentheses [Colour figure can be viewed at wileyonlinelibrary.com]
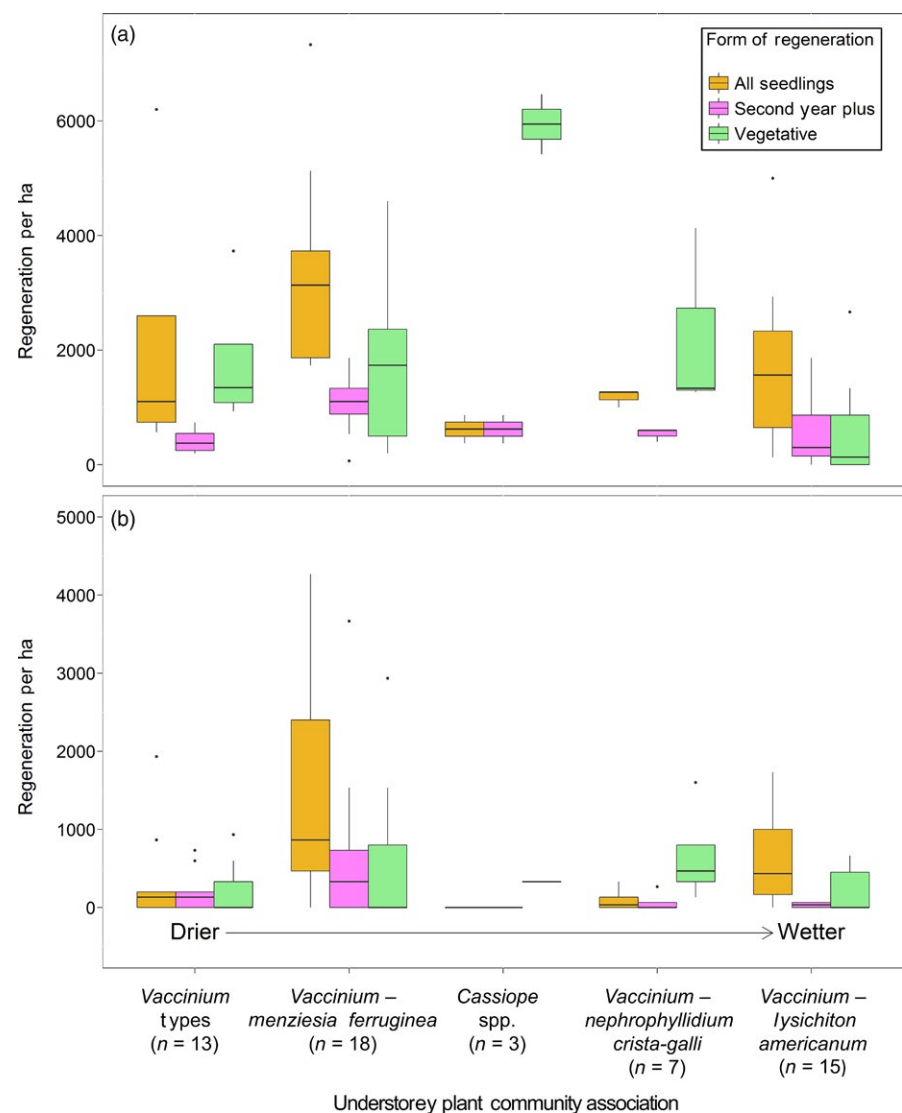
Vegetative regeneration, on the other hand, was most abundant (*M* = 5,944 per ha) in the two interior subplots dominated by *Cassiope* spp.; this plant association is common where snow-loading can lead to increased incidence of vegetative layering in yellow-cedar (Hennon et al., 2016). Vegetative regeneration densities were also abundant in all remaining plant associations in interior subplots (Figure 6a); it was less common, but still prevalent, in the blueberry—skunk cabbage association.

3.5 | Yellow-cedar seedling densities by snow cover

Increasing snow cover was not significantly correlated with seedling and second year plus seedling densities in both exterior and interior subplots (Figure S1). Vegetative regeneration, on the other hand, was strongly correlated with increasing snow cover in interior subplots (ρ = 0.76, *p* = <.01), with no significant relationship observed in exterior subplots.

4 | DISCUSSION

4.1 | Lack of seedling maturation and spread

At this north-eastern range edge, yellow-cedar is generating adequate quantities of seed to produce thousands of germinants per hectare inside existing stands, and seeds are also successfully spreading beyond many stand boundaries into currently unoccupied forests (765 germinants per hectare in exterior plots) (Table 3). 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 of the species (Hennon et al., 2016). However, few of these germinants appear to be surviving to maturity both inside and outside of stands, indicating broad maturation failure regardless of location. Three regional plant community publications for southeast Alaska all note a similar lack of yellow-cedar regeneration from seed in closed canopy forests in the recent past (DeMeo, Martin, & West, 1992; Martin et al., 1995; Pawuk & Kissinger, 1989).

One hypothesis proposed for the lack of yellow-cedar regeneration in the Alexander Archipelago region of Alaska is high browse pressure by Sitka black-tailed deer (Hennon et al., 2016; Martin et al., 1995) and moose (personal observation). We did not observe a substantial percentage of seedlings or vegetative regeneration that had been browsed by deer or moose (data not shown), but it is possible that ungulates are removing entire first and second year seedlings, whose foliage is highly palatable, from the forest during the fall—spring season when preferred deciduous forage is not available. Persistent winter snow cover may offer protection for yellow-cedar seedlings from ungulate browse, and snowier conditions during the Little Ice Age climate period (*c.* 1,100–1,850) may have also kept regional deer populations in check (White, Pendleton, & Hood, 2009). Diminishing snowpacks in recent decades may allow an increasing number of ungulates more access to yellow-cedar seedlings in the late winter and early spring.

Additionally, persistent, insulating snow cover, which is known to protect yellow-cedar roots from freezing injury leading to yellow-cedar decline (Schaberg, D'Amore, Hennon, Halman, & Hawley, 2011), may be equally important for protecting juvenile foliage from freezing events (Hawkins et al., 1994; Russell et al., 1990). Although we did not see higher seedling densities in snowier locations (Figure S1), it is possible that the coarse resolution of the MODIS snow record used (500 m pixels) obscured plot level snow trends. In the dense, closed canopy forests of southeast Alaska, more detailed, site-specific snow cover measurements may be needed for fine scale comparisons to regeneration.

Seed dispersal distance into intact, unoccupied forest was unexpectedly short (4.65 m from stand edges). It is estimated that yellow-cedar require at least 7 years to reach sexual maturity (Hennon et al., 2016); at a high-end assumption of full success of every seedling reaching sexual maturity within 7 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). The isolated stands of mature trees we find, surrounded by other forest types, suggests the latter. Because there is currently a lack of published information on yellow-cedar seed dispersal distances (Hennon et al., 2016), and our study was limited to a germinant analysis, future studies should focus on quantifying actual dispersal capacity of yellow-cedar seeds across forest conditions (open to closed canopy). Better estimates of seed dispersal potential could inform more precise modelling efforts of expected migration into abundant, unoccupied habitat at the range edge (Krapek et al., 2017).

It is possible that site-specific factors such as soil fertility (D'Amore et al., 2009) or parent material are also responsible for yellow-cedar's limited expansion beyond current stand boundaries. In other words, stands may have already fully occupied local niches, and expansion of yellow-cedar on the landscape could be limited to colonization in discrete new portions of the landscape not yet reached by seeds. However, findings on abundant modelled habitat and a pulse of expansion during the Little Ice Age climate period (Krapek et al., 2017), in addition to successful experimental plantings in the region (approximately 1 km from some of the stands) where light and snow conditions are favourable (Hennon et al., 2016), indicate that stands may also have the potential to expand locally.

4.2 | Persistence via vegetative regeneration

Vegetative layering, the opportunistic sprouting of lower limbs via adventitious roots that come into contact with soil, is a common trait among temperate trees adapted to low light levels and particularly to conifers growing in harsh conditions (Del Tredici, 2001). Allocation of resources to sprouting vs. seed production is an important life-history trade-off: sprouting allows for a maximization of local site occupancy, especially on poor site conditions, but sprouters tend to be less competitive from seed (Bellingham & Sparrow, 2000; Vesk & Westoby,

2004). Even if population sizes are small, sprouters are likely more resistant to disturbances and long periods unfavourable for reproduction by seed because sprouting extends generation times and opportunities for sexual reproduction when conditions become favourable (Bellingham & Sparrow, 2000; Bond & Midgley, 2001).

In contrast to yellow-cedar regeneration from seed, vegetative layering was common on all plots (1,688 per ha in interior subplots; Table 3), and across a wide range of understorey plant community and drainage 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 unfavourable for sexual reproduction. Yellow-cedar is an extremely long-lived (>1,000 years; Laroque & Smith, 1999) and stress-tolerant species (Antos et al., 2016) whose high survivorship (Lertzman, 1995) may allow it to persist and "wait" for abiotic (e.g., snowy periods) and/or biotic (e.g., canopy gaps, low deer populations) conditions favourable for regeneration (Bond & Midgley, 2001).

4.3 | Stalled stand development

Diameter distributions of yellow-cedar trees in stand edge plots and the three fully stem-mapped stands further support the lack of yellow-cedar spread over the last century or longer. Stand edge subplots showed a similar diameter distribution to fully mapped stands, both of which included a few large overstorey trees and a "reverse-j"-shaped diameter distribution, indicative of old growth conditions (Deal, Oliver, & Bormann, 1991). If stands were actively spreading into what appears to be suitable habitat in the study area (see habitat modelling in Krapek et al., 2017), we would expect to see a gradient of larger, older trees near points of establishment to smaller, younger trees located near at least some expanding stand edges. Instead, 86- to 383-year-old (median = 199-year-old) yellow-cedar trees are located within 15 m of stand boundaries; in some cases, these trees are located abruptly at stand boundaries (see Figures 3 and 7). Therefore, the average stand edge has moved less than 15 m since the early 1800s, which coincides approximately with the final decades of the colder and potentially snowier Little Ice Age period (Wiles et al., 2014). Hennon et al. (1990) and Beier, Sink, Hennon, D'Amore, and Juday (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 period conducive to yellow-cedar establishment across the region. 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 up to 100 year after death or persist for decades on the forest floor following bole breakage (Hennon et al., 2016); therefore we would have expected to see dead trees if stands had contracted in the recent past.

4.4 | Plant community controls on regeneration

Yellow-cedar seedlings were strongly clustered with each other at short distances (1 and 2 m), while they showed a slight tendency, though variable, of inhibition from overstorey trees at all lag distances (1–4 m)

FIGURE 7 Photograph of a typical yellow-cedar stand boundary in the study area. Approximately 200-year-old yellow-cedar (*Callitropsis nootkatensis*) are located abruptly at the stand edge, with regeneration of other tree species (e.g., western hemlock *[Tsuga heterophylla]*) 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. This stand is the East Glacier population listed in Figure 1 [Colour figure can be viewed at wileyonlinelibrary.com]

when significant spatial relationships were observed. Yellow-cedar is known to be relatively shade intolerant compared to sympatric conifers in the region (Hennon et al., 2016) and therefore may have been negatively associated with overstorey trees 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 favourable microsites for germination with higher nutrients. Plots with the highest densities of germinants and second year plus seedlings tended to have more open canopies (personal observation), although light transmittance was not measured and should be considered in future studies. Seedlings planted at a common garden on a former clearcut within the study area (see cross symbol in Figure 1) are currently growing rapidly in high-light conditions and an area of substantial snow accumulation (Hennon et al., 2016) indicating that, once established, yellow-cedar are well-adapted to grow in additional habitat across the northern range edge.

Regeneration from seed, and survival past the germinant phase, was most common in blueberry—false azalea understories; *Menziesia* is an indicator species for higher light understorey conditions in the region (Martin et al., 1995). The well-drained soils in this community may additionally aid seedling development as seedlings are able to root more deeply and better access available nutrients. *Menziesia* shrubs are eaten in small quantities compared to blueberry shrubs (Hanley & McKendrick, 1985; McClellan, Hennon, Heuer, & Coffin, 2014); therefore, high *Menziesia* coverage possibly indicates lower deer usage of that community type, also aiding yellow-cedar establishment.

Large quantities of seed were also observed in the skunk cabbage-dominated understorey plant association, which may also have higher light transmittance to the understorey. Skunk cabbage associations have the highest percentage of poorly drained soils (Table 2), indicating that light may be relatively be more important than soil type for seedling success.

4.5 | Migration capacity of yellow-cedar under current climate and forest condtions

Jackson et al. (2009) discuss how long-term environmental variability creates a ratchet mechanism controlling the invasion of many long-lived woody plants, with periods of rapid colonization and expansion when conditions are favourable, followed by persistence when conditions are not. With temporally varied pulses of successful recruitment and dispersal to new habitats via seed across centuries to millennia, distributions of species are the result of multiple, interacting climatic and biotic constraints (Gouveia, Hortal, Cassemiro, Rangel, & Diniz-Filho, 2013; Walther et al., 2002). Our results indicate that yellow-cedar's ongoing migration and colonization of new habitat at the leading north-eastern range edge is currently in a lull after a pulse of expansion during the Little Ice Age, and lags behind suitable climate and forest conditions for yellow-cedar growth (Krapek et al., 2017). Characterizing species migration lags is essential for creating accurate models to predict future species distributions under changing climate (Johnstone & Chapin, 2003).

While the abiotic condition does not appear to be limiting (*sensu* Soberon & Peterson, 2005), the interaction between snow conditions (seedling protection) and forest composition (light regime) may be important in controlling the rate of successful dispersal. Ultimately, these abiotic and biotic factors interact to influence migration: increased snow cover during cool periods may reduce ungulate browse (Hennon et al., 2016) and increased snow loading on trees could lead to higher bole breakage and crown damage (Päätalo, Peltola, & Kellomäki, 1999), opening the forest canopy and creating light regimes more favourable to yellow-cedar. In addition to its importance for protecting adult trees from freezing injury, snow may be equally important for yellow-cedar regeneration and expansion on the landscape, with cold, moist intervals promoting regeneration.

Preliminary molecular DNA work from foliage collections across the entire yellow-cedar range suggests the species expanded at an exponential rate across Alaska at some point in the past (Hennon et al., 2016), further supporting an episodic migration history for the species. The oldest radiocarbon dated pollen records indicate that yellow-cedar only became abundant in southeast Alaska over the past 5,000 years during the neoglacial cooling period (Ager, Carrara, Smith, Anne, & Johnson, 2010; Hansen & Engstrom, 1996), with snowy periods within this interval potentially favouring yellow-cedar colonization. Future studies in which light, snow and soil nutrients are experimentally manipulated will be necessary to determine the precise mechanisms controlling successful development of yellow-cedar seedlings to tree stage, which currently appears limited in natural populations. Ungulate exclusion studies should be conducted to help determine if browse pressure was eliminating entire first and second year seedlings from the forest floor before they had time to develop mature, less palatable foliage (Hennon et al., 2016).

5 | CONCLUSIONS

This is the first study to quantify northward range expansion in yellow-cedar, which is concurrently experiencing mass mortality in some warmer, southward portions of its range. At leading edge stand boundaries, yellow-cedar seedling success and spread is unexpectedly limited, considering non-limiting climate and plant community conditions similar to established yellow-cedar forests elsewhere in the range. Seeds are germinating, but few are surviving to tree stage, and dispersal distance is low. Large, *c.* 100–200-year-old trees are located abruptly at stand boundaries, indicating that the geographic extent of stands has been relatively static since the end of the Little Ice Age.

Where seedlings were observed, densities varied by plant community, with the most seedlings located in understories indicative of high-light conditions. Seedlings also showed slight negative spatial relationships with the three dominant overstorey tree species, including yellow-cedar. Lack of light under in closed canopy stands may be one factor contributing to yellow-cedar regeneration failure observed in the region. Vegetative regeneration, common across all stands, may be an adaptive strategy that allows yellow-cedar to persist on the landscape in periods that are unfavourable for seedling growth. However, vegetative regeneration will not actively push the range edge forward compared to dispersal of seed to new habitats.

If we considered climate and potential habitat only, it would seem that the yellow-cedar range might be able to shift north, as it experiences waves of mortality farther south. However, this study highlights that a species' dispersal capacity and competitive ability across temporally varied climatic conditions are important considerations in ultimately predicting a species' migration capacity.

AUTHORS' CONTRIBUTIONS

B.B. conceived the ideas; B.B. and J.K. designed the methodology, and collected and analysed the data; J.K. led the writing with contributions from B.B.

DATA ACCESSIBILITY

Yellow-cedar stand geographic data and stem map plot data are available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.7rd7s) (Krapek & Buma, 2017). Snow data are available at: http://www.gina.alaska.edu/projects/modis-derived-snow-metrics.

ORCID

John Krapek 🔘 http://orcid.org/0000-0002-4435-4113

Brian Buma 🔘 http://orcid.org/0000-0003-2402-7737

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*, 259–268. https://doi.org/10.1016/j.yqres.2009.12.005

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. https://doi.org/10.1016/j.foreco.2016.05.043

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*, 477–489. https://doi.org/10.1890/13-2042.1

Baddeley, A., Rubak, E., & Turner, R. (2015). *Spatial point patterns: Methodology and applications with R*. London, UK: Chapman and Hall/CRC Press. Retrived from 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*, 1319–1334. https://doi.org/10.1139/X07-240

Bellingham, P. J., & Sparrow, A. D. (2000). Resprouting as a life history strategy in woody plant communities. *Oikos*, *89*, 409–416. https://doi.org/10.1034/j.1600-0706.2000.890224.x

Besag, J. (1977). Contribution to the discussion of Dr. Ripley's paper. *Journal of the Royal Statistical Society, Series B*, *39*, 193–195.

Bond, W. J., & Midgley, J. J. (2001). Ecology of sprouting in woody plants: The persistence niche. *Trends in Ecology & Evolution*, *16*, 45–51. https://doi.org/10.1016/S0169-5347(00)02033-4

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*, *27*, 597–623. https://doi.org/10.1146/annurev.ecolsys.27.1.597

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*, 3445–3454. https://doi.org/10.1111/gcb.12915

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.

Buma, B., Hennon, P. E., Harrington, C. A., Popkin, J. R., Krapek, J., Lamb, M. 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*, *23*, 2903–2914.

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*, 844–854. https://doi.org/10.1139/cjfr-2016-0041

Burns, R. M., & Honkala, B. H. (1990). *Silvics of North America. Volume 1. Conifers, agriculture handbook No. 654*. Washington, DC: U.S. Department of Agriculture, Forest Service.

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*, 1024–1026. https://doi.org/10.1126/science.1206432

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*, 2261–2268. https://doi.org/10.1016/j.foreco.2009.03.006

Davis, M. B., & Shaw, R. G. (2001). Range shifts and adaptive responses to quaternary climate change. *Science*, *292*, 673–679. https://doi.org/10.1126/science.292.5517.673

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*, 643–654. https://doi.org/10.1139/x91-088

Del Tredici, P. (2001). Sprouting in temperate trees: A morphological and ecological review. *The Botanical Review*, *67*, 121–140. https://doi.org/10.1007/BF02858075

DeMeo, T., Martin, J., & West, R. A. (1992). *Forest plant association management guide: Ketchikan area, Tongass National Forest*. Ketchikan, Alaska: US Forest Service, Tongass National Forest.

Dewey, M. (2017). metap: Meta-analysis of significance values. R package version 0.8.

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*, 53–64. https://doi.org/10.1046/j.1466-822X.2003.00322.x

Dubois, G., & Burr, S. (2015). FS-R10-FHP. Forest Health Conditions in Alaska 2015. Anchorage, AK. U.S. Forest Service, Alaska Region. Publication R10-PR-38.

Gouveia, S. F., Hortal, J., Cassemiro, F. A., Rangel, T. F., & Diniz-Filho, J. A. F. (2013). Nonstationary effects of productivity, seasonality, and historical climate changes on global amphibian diversity. *Ecography*, *36*, 104–113. https://doi.org/10.1111/j.1600-0587.2012.07553.x

Griffith, D. A. (1987). *Spatial autocorrelation, a primer*. Resource publications in geography. Washington, DC: Association of American Geographers.

Hanley, T. A., & McKendrick, J. D. (1985). Potential nutritional limitations for black-tailed deer in a spruce-hemlock forest, Southeastern Alaska. *The Journal of Wildlife Management*, *49*, 103–114. https://doi.org/10.2307/3801853

Hansen, B. C., & Engstrom, D. R. (1996). Vegetation history of Pleasant Island, southeastern Alaska, since 13,000 yr BP. *Quaternary Research*, *46*, 161–175. https://doi.org/10.1006/qres.1996.0056

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*, 945–953. https://doi.org/10.1139/x94-124

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*, 147–158. https://doi.org/10.1525/bio.2012.62.2.8

Hennon, P. E., McKenzie, C. M., D'Amore, D. V., Wittwer, D. T., Mulvey, R. L., Lamb, M. S., ... Cronn, R. C. (2016). *A climate adaptation strategy for conservation and management of yellow-cedar in Alaska*. PNW-GTR-917. Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Hennon, P. E., Shaw, C. G., & Hansen, E. M. (1990). Dating decline and mortality of *Chamaecyparis nootkatensis* in southeast Alaska. *Forest Science*, *36*, 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. *Northwest Science*, *75*, 61–71.

Ibáñez, I., Clark, J. S., & Dietze, M. C. (2009). Estimating colonization potential of migrant tree species. *Global Change Biology*, *15*, 1173–1188.

Jackson, S. T., Betancourt, J. L., Booth, R. K., & Gray, S. T. (2009). Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 19685–19692. https://doi.org/10.1073/pnas.0901644106

Johnstone, J. F., & Chapin, F. S. (2003). Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. *Global Change Biology*, *9*, 1401–1409. https://doi.org/10.1046/j.1365-2486.2003.00661.x

Krapek, J., & Buma, B. (2017). Data from: Limited stand expansion by a long-lived conifer at a leading northern range edge, despite available habitat. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.7rd7s

Krapek, J., Hennon, P. E., D'Amore, D. V., & Buma, B. (2017). Despite available habitat at range edge, yellow-cedar migration is punctuated with a past pulse tied to colder conditions. *Diversity and Distributions*, https://doi.org/10.1111/ddi.12630

Laroque, C. P., & Smith, D. J. (1999). Tree-ring analysis of yellow-cedar (*Chamaecyparis nootkatensis*) on Vancouver Island, British Columbia. *Canadian Journal of Forest Research*, *29*, 115–123. https://doi.org/10.1139/x98-185

Lertzman, K. P. (1995). Forest dynamics, differential mortality and variable recruitment probabilities. *Journal of Vegetation Science*, *6*, 191–204. https://doi.org/10.2307/3236214

Lindsay, C., Zhu, J., Miller, A. E., Kirchner, P., & Wilson, T. L. (2015). Deriving snow cover metrics for Alaska from MODIS. *Remote Sensing*, *7*, 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*, 1052–1055. https://doi.org/10.1038/nature08649

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. Juneau, AK: USDA Forest Service.

McClellan, M. H., Hennon, P. E., Heuer, P. G., & Coffin, K. W. (2014). Condition and deterioration rate of precommercial thinning slash at False Island, Alaska. Res. Pap. PNW-RP-594. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 29 p.

McLachlan, J. S., Clark, J. S., & Manos, P. S. (2005). Molecular indicators of tree migration capacity under rapid climate change. *Ecology*, *86*, 2088–2098. https://doi.org/10.1890/04-1036

Morin, X., & Thuiller, W. (2009). Comparing niche-and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology*, *90*, 1301–1313. https://doi.org/10.1890/08-0134.1

National Oceanic and Atmospheric Administration. (2016). Juneau International Airport Climate Data. Available at: http://pajk.arh.noaa.gov/.

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*, 271–291. https://doi.org/10.1016/S0378-1127(01)00436-4

Päätalo, M. L., Peltola, H., & Kellomäki, S. (1999). Modelling the risk of snow damage to forests under short-term snow loading. *Forest Ecology and Management*, *116*, 51–70. https://doi.org/10.1016/S0378-1127(98)00446-0

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*, 389–401. https://doi.org/10.1016/j.biocon.2004.12.006

Peteet, D. M. (2000). Sensitivity and rapidity of vegetational response to abrupt climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *97*, 1359–1361. https://doi.org/10.1073/pnas.97.4.1359

Petit, R. J., Hu, F. S., & Dick, C. W. (2008). Forests of the past: A window to future changes. *Science*, *320*, 1450–1452. https://doi.org/10.1126/science.1155457

Pulliam, H. R. (1988). Sources, sinks, and population regulation. *The American Naturalist*, *132*, 652–661. https://doi.org/10.1086/284880

Ripley, B. D. (1977). Modelling spatial patterns. *Journal of the Royal Statistical Society*, *Series B*, *39*, 172–212.

Ritland, C., Pape, T., & Ritland, K. (2001). Genetic structure of yellow cedar (*Chamaecyparis nootkatensis*). *Canadian Journal of Botany*, *79*, 822–828.

Russell, J., Grossnickle, S. C., Ferguson, C., & Carson, D. W. (1990). *Yellow-cedar stecklings: Nursery production and field performance*. FRDA Report, Victoria, B.C., No.148 pp.20 pp. ref.2

Sax, D. F., Early, R., & Bellemare, J. (2013). Niche syndromes, species extinction risks, and management under climate change. *Trends in Ecology & Evolution*, *28*, 517–523. https://doi.org/10.1016/j.tree.2013.05.010

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*, 2142–2150. https://doi.org/10.1016/j.foreco.2011.08.004

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*, 1282–1293. https://doi.org/10.1111/j.1365-2486.2008.01577.x

Scheele, B. C., Foster, C. N., Banks, S. C., & Lindenmayer, D. B. (2017). Niche contractions in declining species: Mechanisms and consequences. *Trends in Ecology & Evolution*, *32*, 346–355. https://doi.org/10.1016/j.tree.2017.02.013

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. https://doi.org/10.1146/annurev.ecolsys.110308.120317

Soberon, J., & Peterson, A. T. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, *2*, 1–10.

Stokes, M. A., & Smiley, T. L. (1968). *Tree-ring dating*. Chicago, IL: University of Chicago Press.

Van der Knaap, W. O., van Leeuwen, J. F., Finsinger, W., Gobet, E., Pini, R., Schweizer, A., … Ammann, B. (2005). Migration and population expansion of Abies, Fagus, Picea, and Quercus since 15,000 years in and across the Alps, based on pollen-percentage threshold values. *Quaternary Science Reviews*, *24*, 645–680. https://doi.org/10.1016/j.quascirev.2004.06.013

Vesk, P. A., & Westoby, M. (2004). Sprouting ability across diverse disturbances and vegetation types worldwide. *Journal of Ecology*, *92*, 310–320. https://doi.org/10.1111/j.0022-0477.2004.00871.x

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*, 2145–2161. https://doi.org/10.1111/j.1365-2486.2010.02368.x

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., … Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, *416*, 389–395. https://doi.org/10.1038/416389a

White, K. S., Pendleton, G. W., & Hood, E., (2009). Effects of snow on Sitka black-tailed deer browse availability and nutritional carrying capacity in southeastern Alaska. *Journal of Wildlife Management*, *73*, 481–487.

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 1,200 years. *The Holocene*, *40*, 198–208. https://doi.org/10.1177/0959683613516815

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*, 1042–1052. https://doi.org/10.1111/j.1365-2486.2011.02571.x

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