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Despite available habitat at range edge, yellow-cedar migration is punctuated with a past pulse tied to colder conditions

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Abstract

Aim: To explore the recent (past ~1,000 year) migration history of yellow-cedar (*Callitropsis nootkatensis*), a climate-threatened tree, which appears to lag behind its potential climatic niche at a leading northern range edge, and infer its continued migration potential under changing climate.

Location: Southeast Alaska, USA.

Methods: We located 11 leading range edge yellow-cedar stands near Juneau, Alaska, determined their proportional occupancy of modelled habitat and estimated stand ages to determine approximate time of establishment. We used future climate projections to determine the potential vulnerability of these leading edge populations using a well-established risk factor for yellow-cedar mortality in the region.

Results: Despite abundant potential habitat, and having existed in the study area > 675 years, yellow-cedar has only occupied a small proportion (<0.8%) of suitable habitat. Yellow-cedar appears to have undergone a past pulse of successful regeneration and establishment during the Little Ice Age climate period, with little expansion in recent decades. Under high emissions future climate scenarios, nine of 11 stands (82%) may become exposed to climate conditions that predispose yellow-cedar to root freezing injury by 2070.

Main conclusions: We show that yellow-cedar's migration near a northern range edge is episodic, with a past pulse of establishment during the Little Ice Age. When planning for the conservation and management of this culturally and economically valuable tree, forest managers should consider yellow-cedar's currently limited migration at the leading edge, mortality emerging farther north in recent decades and potential vulnerability of range edge stands by 2070. The range of intense, climatic driven yellow-cedar mortality is expanding northward and rapidly approaching the species' leading edge in southeast Alaska. Yellow-cedar's episodic migration demonstrates that species may not respond linearly to a warming climate and that other factors controlling dispersal to suitable habitat must be considered for accurate range predictions.

KEYWORDS
assisted migration, climate change, migration lag, punctuated migration, range expansion, vulnerability assessment, yellow-cedar

1 | INTRODUCTION

Determining the rate of species spread at leading range edges, and contraction at trailing edges, is a critical research and conservation concern in an era of rapidly shifting climatic niches (Loarie et al., 2009). Numerous studies have shown that plant species are already moving poleward and uphill at rapid rates in response to climate warming (Parmesan & Yohe, 2003), but rates of migration may not keep pace with rates of change (Hille Ris Lambers et al., 2015; Loarie et al., 2009; Zhu, Woodall, & Clark, 2012), particularly for long-lived conifers with extended generation times (Jackson et al., 2009). Characterizing the potential niche space for migrating species, while determining their actual dispersal capacity to reach that space under shifting abiotic conditions, will be essential for predicting natural migration potentials (Feurdean et al., 2013; Franklin, Serra-Diaz, Syphard, & Regan, 2016).

The palaeobotanical 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 shifts (Ordonez & Williams, 2013). However, the fossil pollen record can be a blunt tool which may miss the presence of small, low-density populations (McLachlan, Clark, & Manos, 2005; Pearson, 2006) or overestimate the presence of local taxa (Peteet, 1986). Studying modern tree migrations, on the other hand, may ultimately allow for more accurate inferences in the near term. As species around the world are threatened with global change-related range reductions and extirpations, developing comprehensive approaches to predict future distributions will be critical for biodiversity conservation. (Aitken, Yeaman, Holliday, Wang, & Curtis-McLane, 2008; Dawson, Jackson, House, Prentice, & Mace, 2011; Pressey, 2004). Precise delineations of actively shifting ranges and understanding of past migration rates are critical for biodiversity conservation in a warming world (Huntley, 1991).

Yellow-cedar (*Callitropsis nootkatensis* D. Don; Oerst. ex D.P. Little) is a long-lived conifer of the northern Pacific coastal temperate rainforest (PCTR) region that is hypothesized to be undergoing a continued natural range expansion (Hennon, D'Amore, Schaberg, Wittwer, & Shanley, 2012) since the end of the Last Glacial Maximum (LGM) ca. 20,000 years before present. Yellow-cedar is absent in some forests in southeast Alaska despite what appears to be suitable habitat (Martin, Trull, Brady, West, & Downs, 1995) and its migration following deglaciation is not fully understood (Hennon et al., 2016). Except for the presence of yellow-cedar, plant community composition, climate, soils and geomorphology are otherwise similar between yellow-cedar and many non-yellow-cedar forests (e.g., *Tsuga*-dominated communities; Martin et al., 1995; Hennon et al., 2016), suggesting that competition and abiotic conditions are not precluding yellow-cedar growth.

In addition to apparent dis-equilibrium with climate and ongoing migration potential at its northern range edge, yellow-cedar forests in southeast Alaska and British Columbia are experiencing widespread mortality (~400,000 ha; Buma et al., 2016), known as "yellow-cedar decline" (YCD), related to climate changes since the end of the Little Ice Age (LIA; Hennon et al., 2012). Typically, more than 70% (by basal area) of a yellow-cedar population dies in these decline events. Diminishing winter snowpacks, which are critical for protecting yellow-cedar's shallow fine roots from freezing air temperatures, is the primary predisposing cause of yellow-cedar mortality (Schaberg, D'Amore, Hennon, Halman, & Hawley, 2011). Average winter temperatures in Southeast Alaska have historically been close to freezing (0°C). Under climate change, snowpacks will be further diminished with even minor winter temperature increases (Shanley et al., 2015), exposing new portions of the yellow-cedar range to sporadic winter freezing events (Hennon et al., 2016). Yellow-cedar decline has been observed only 100 km south of the current north-east range edge (Dubois & Burr, 2015).

With the range of intense, climate-driven yellow-cedar mortality approaching its leading edge of natural expansion in southeast Alaska, determining whether yellow-cedar range has the inherent migration potential to keep pace with shifting climate is a critical research and conservation question. Yellow-cedar is a unique example of a species migrating through relatively intact, undisturbed habitats, which is an important comparison to studies of species range shifts through more developed landscapes with significant human influence (Zhu et al., 2012). As species' leading and trailing edges converge under rapidly shifting climate, precise on-the-ground delineations of recent range edge expansion will provide the clearest window into future migration capacity.

1.1 | Objectives

Our objective in this study was to locate leading range edge yellow-cedar stands and answer the following questions:

1. When did leading range edge yellow-cedar populations establish, and is the species actively colonizing new habitat?
2. Does additional suitable habitat exist on the landscape for continued yellow-cedar expansion? Or, has yellow-cedar filled its potential niche in the region?
3. Will leading edge stands become vulnerable to YCD in future climate scenarios?

2 | METHODS

2.1 | Study area description

The study area is located near Juneau, Alaska, USA, beyond yellow-cedar's contiguous north-east range edge (Figure 1). Juneau's climate is cool maritime despite its high latitude (58°N), caused by the moderating influence of the Pacific Ocean's Alaska current (Martin et al., 1995). Mean monthly temperatures range from −2 to 14°C at sea level (NOAA, 2016), but strong topographic gradients cause significant temperature variability at fine scales. Precipitation ranges from 1,000 to >5,000 mm annually with no summer drought period, and during mild years, low-elevation areas remain snow-free for much of the winter (Martin et al., 1995). This leads to a landscape relatively free from widespread natural disturbances (e.g., fire, large insect outbreaks), creating a mosaic of late seral forests, peatlands and shrublands (Martin et al., 1995). The predominant disturbance is localized windthrow,

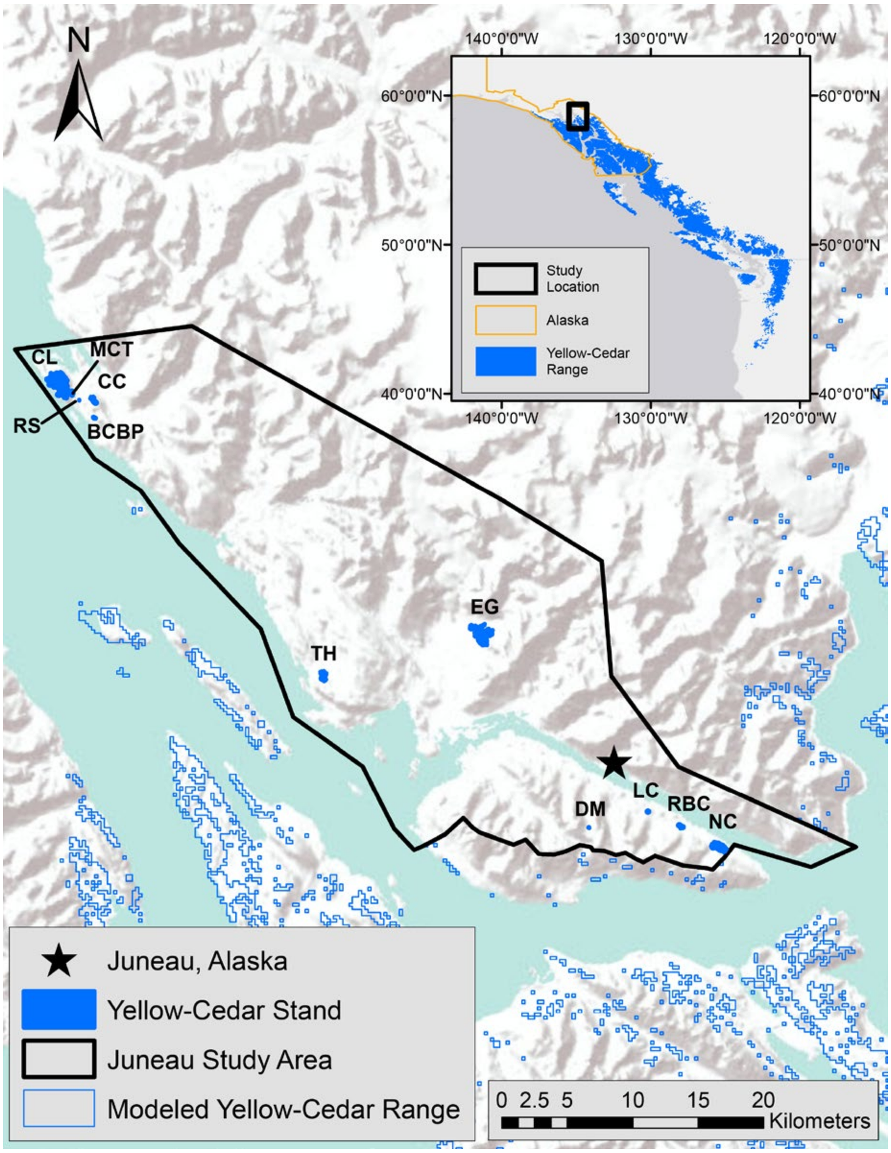

FIGURE 1 Yellow-cedar stands in study area near Juneau, Alaska. Map inset shows study area location in context of yellow-cedar's range (Buma et al., 2016). These leading edge stands appear to be at the front of a directional migration northward into suitable habitat in the region and are located ahead of the continuous range farther south. 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: 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

consisting of generally <1,000 m^2 patches (Buma & Barrett, 2015; Ott & Juday, 2002) with a very long return interval (>1,000 years); occasional stand-replacing blowdowns or localized landslides may occur with extreme wind and precipitation events (Nowacki & Kramer, 1998). There is no significant logging history in the study area in recent decades.

Tree diversity is low, with western hemlock (*Tsuga heterophylla* Raf., Sarg.) and Sitka spruce (*Picea sitchensis* Bong., Carrière) dominating most of the moderate to well-drained, stable sites; mountain hemlock (*T. mertensiana* Bong., Carrière) replaces western hemlock in the subalpine zone (Martin et al., 1995). Yellow-cedar and mountain and western hemlocks can co-dominate on stable, moderately to marginally productive sites with poor drainage and/or shallow soils.

2.2 | Yellow-cedar occurrence mapping and tree ages

Eleven (11) yellow-cedar stands, defined as groups of yellow-cedar trees (in one case a single tree isolated from other stands by >2.5 km) within the forest community and with >250 m separation between groups of yellow-cedar, were identified via a combination of previous US Forest Service (USFS) mapping, community knowledge and a helicopter survey of the study area. On the ground, we delineated stands by recording GPS coordinates approximately every 10 m along the boundary of mature yellow-cedar trees (>1.4 m in diameter at breast height [DBH]).

Isolated individual trees, or group of trees, >30 m from the main stand boundary were considered a separate occurrence. We used 30 m as a limit for considering a lone tree or group as separate from the main stand because mature yellow-cedar trees are approximately 30 m in height, on average, and there is currently a lack of published information on average seed dispersal distance for the species. There are no known avian dispersers (Hennon et al., 2016). In a companion study on the regeneration and spread of yellow-cedar seedlings into unoccupied forests, average seed dispersal distance was observed to be <5 m (29 locations spread over eight of the stands described here; Krapek & Buma, in revision). Within the 11 stands, we mapped 27

TABLE 1 GIS data layers and sources for yellow-cedar habitat analysis and modelling in Juneau, Alaska study area

Data layer	Source
Aspect Compound topographic index Elevation Slope Solar radiation	IfSAR DEM; U.S. Geological Survey (2015)
Mean annual temperature	WorldClim; Hijmans et al. (2005)
Snow Continuous snow season duration Day of last snow in continuous snow season Total snow days in continuous snow season	GINA; Lindsay et al. (2015)
Wind exposure index	Buma and Barrett (2015)

groups and 14 lone trees, for a total of 41 independent "occurrences," or incidents of known establishment and spread (as opposed to vegetative regeneration).

The 11 stands were compared as a unit for establishment age. Increment cores were taken from 10 of 11 stands. Trees were cored approximately one metre above the ground and aged using standard methods (Stokes & Smiley, 1968). Because stands range in size from a single tree (smallest) to over 150 ha (largest) in size, we sampled proportionally more trees in smaller than larger stands. 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 due to lack of published correction factors; therefore, stand ages reported here are underestimated.

2.3 | Topographic GIS analysis of yellow-cedar occurrences

We examined ten landscape variables (five topographic, three snow cover, one disturbance metric (wind exposure) and mean annual temperature; Table 1) to compare the landscape features where yellow-cedar occurs to locations where it is not known to be present. These variables were chosen because topography, specifically elevation and factors related to water accumulation (slope, contributing area), is a strong control on climate, forest productivity and plant community composition in the region (Caouette et al., 2016) and could influence establishment.

For topographically derived variables, we utilized an interferometric synthetic aperture radar (IfSAR) bare-earth digital elevation model (5 m resolution; US Geological Survey, 2015). We derived aspect, compound topographic index, elevation, slope and solar radiation from the DEM. Compound topographic index (CTI), a measure of water accumulation across the landscape, was computed as:

$$\mathrm{CTI} = ln\left(\frac{a}{\tan(b)}\right),$$

where "a" is the upslope contributing area, and "b" is the slope in radians (Gessler, Moore, McKenzie, & Ryan, 1995). Although elevation is a significant control on climate in the study area, we also examined mean annual temperature data (30 arc-second resolution; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) to test the influence of temperature on yellow-cedar establishment.

Lack of snow cover is one of two important risk factors for yellow-cedar decline (Schaberg et al., 2011), and snow may additionally aid yellow-cedar establishment by protecting seedlings from ungulate browse (Hennon et al., 2016). For snow cover 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 (500 m; Lindsay, Zhu, Miller, Kirchner, & Wilson, 2015) for 2001–2014. We used "continuous snow season" (CSS) metrics from Lindsay et al. (2015), which represent 14 day or longer snow cover periods, rather than snow on/off at short intervals. Means and minima were computed for the entire period of snow data available.

Yellow-cedar is a slow-growing tree that is more competitive in high-light conditions in the region (Martin et al., 1995) and may be dependent on disturbance to establish and/or persist in old-growth forests with infrequent canopy turnover. Therefore, we examined a wind exposure index based on topographic sheltering to regional storm tracks from the south-east and south (Buma & 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 & Kramer, 1998).

All lower resolution data layers were resampled using bilinear interpolation to match the 5 m resolution of the IfSAR dataset. Mean values of each landscape variable were calculated for each yellow-cedar occurrence (n = 41) on the landscape.

2.4 | Comparison to areas of yellow-cedar absence

To determine if yellow-cedar establishes within a certain topographic niche on the landscape, we randomly sampled (n = 1,000) the same ten GIS data layers where yellow-cedar was not detected in the study area ("null points"). To constrain the locations of the random null points, we first used the 2011 National Land Cover Database (Homer et al., 2015) to remove non-vegetated pixels from all data layers. Next, we eliminated areas above 593 m in elevation, which is the highest elevation where we observed yellow-cedar. In an analysis of Forest Inventory and Analysis (FIA) plots in the northern Alaskan panhandle, Caouette et al. (2016) found that above 600 m, yellow-cedar presence decreases to below 20%. Finally, we removed the extent of actual yellow-cedar occurrences.

We constructed kernel density plots for each topographic variable sampled using R software (R Development Core Team 2016) to visually 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 of topographic variables were significantly different between occurrences and null points

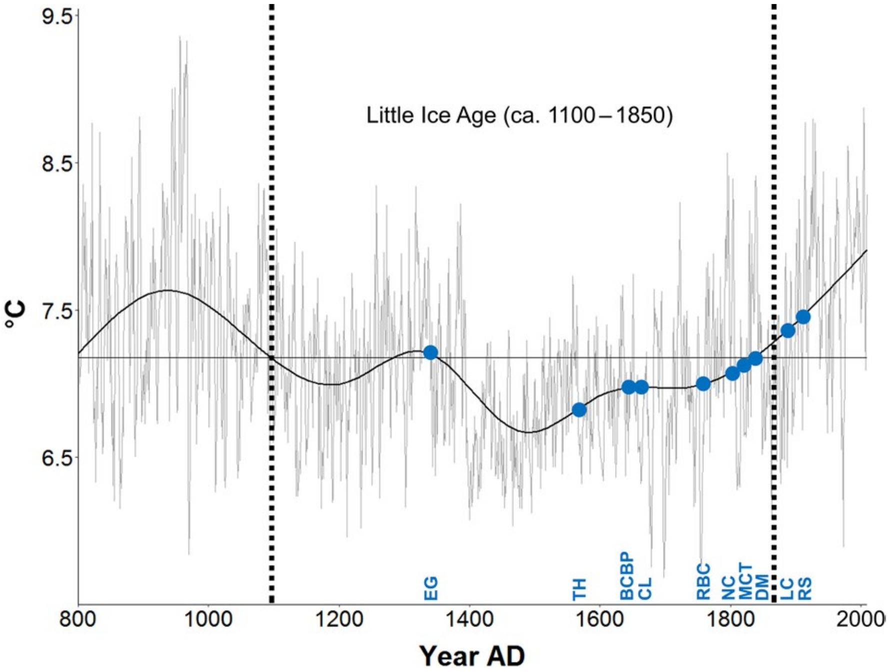

FIGURE 2 Estimated ages for 10 yellow-cedar stands in study area overlaid with a temperature reconstruction for the Gulf of Alaska Region from Wiles et al. (2014). A locally smoothed regression line was added for display of temperature trends. Ages reported are minimum ages (no correction applied for core height or internal decay) and are not necessarily from oldest tree within stand; therefore, each stand age could be underestimated by decades. Dashed vertical lines represent Little Ice Age time period (1100–1850) when most stands established. Stand abbreviations same as Figure 1

($\alpha = 0.05$). We applied a Holm-Bonferroni correction to Kruskal–Wallis tests to control the family-wise error rate.

2.5 | Habitat modelling

Because little work has been performed on modelling potential habitat for species not currently at climatic equilibrium (Veloz et al., 2012), we used two complimentary approaches to estimate potential yellow-cedar habitat. 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 location on the study area landscape that fell within the full range of those variables (i.e., the intersection of current conditions where yellow-cedar grows in the study area or fundamental landscape niche). Second, we used a binomial generalized logistic regression (GLM, logit link) model to identify likely yellow-cedar habitat based on the topographic values at the geographic mean centre of each yellow-cedar occurrence. This approach is useful for identifying likely yellow-cedar habitat based on common landscape features, but does not take into account the fact that yellow-cedar may not be fulfilling its potential niche, and is more restrictive than the intersection method. Together, the two methods are intended to approximately bracket the area of potential yellow-cedar habitat.

2.6 | Vulnerability analysis

To estimate future vulnerability of stands to yellow-cedar decline, we used climate projections for mean winter temperatures (defined as the coldest quarter of the year; Hijmans et al., 2005) as a proxy for future winter snow coverage. A low and high Representative Concentration Pathway (RCP 2.6 and RCP 8.5) emissions scenario from the HadGEM2-ES coupled Earth System Model (Collins et al., 2011) was examined for two bidecadal periods centred 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 successfully applied in regional yellow-cedar decline mapping (Buma et al., 2016). Study area yellow-cedar stands were overlaid with climate projections to determine which stands might be susceptible to future low snow coverage.

3 | RESULTS

3.1 | Yellow-cedar occurrence mapping

Within the 11 yellow-cedar stands (Figure 1), 41 distinct yellow-cedar occurrences were mapped, including 14 lone individuals, and 27 groups of trees ranging in size from <0.01 ha to a 151 ha, totalling 286 ha. Summary statistics for all occurrences are included Table S1 in Appendix S1.

3.2 | Tree ages and stand dynamics

The oldest yellow-cedar stand in the study area was approximately 675 years, although with substantial internal decay of the oldest tree cored, this is an underestimate. The youngest stand had a minimum age of 89 years and is only 0.04 ha in size. The mean age of the 10 stands was 295 years (median = 232). Eight out of ten stands (11th not sampled due to equipment failure) appear to have established during the LIA climate period of 1100–1850 (Wiles et al., 2014; Figure 2). The two stands that established after 1850 are extremely small in extent, consisting of a single tree surrounded by no regeneration, and a

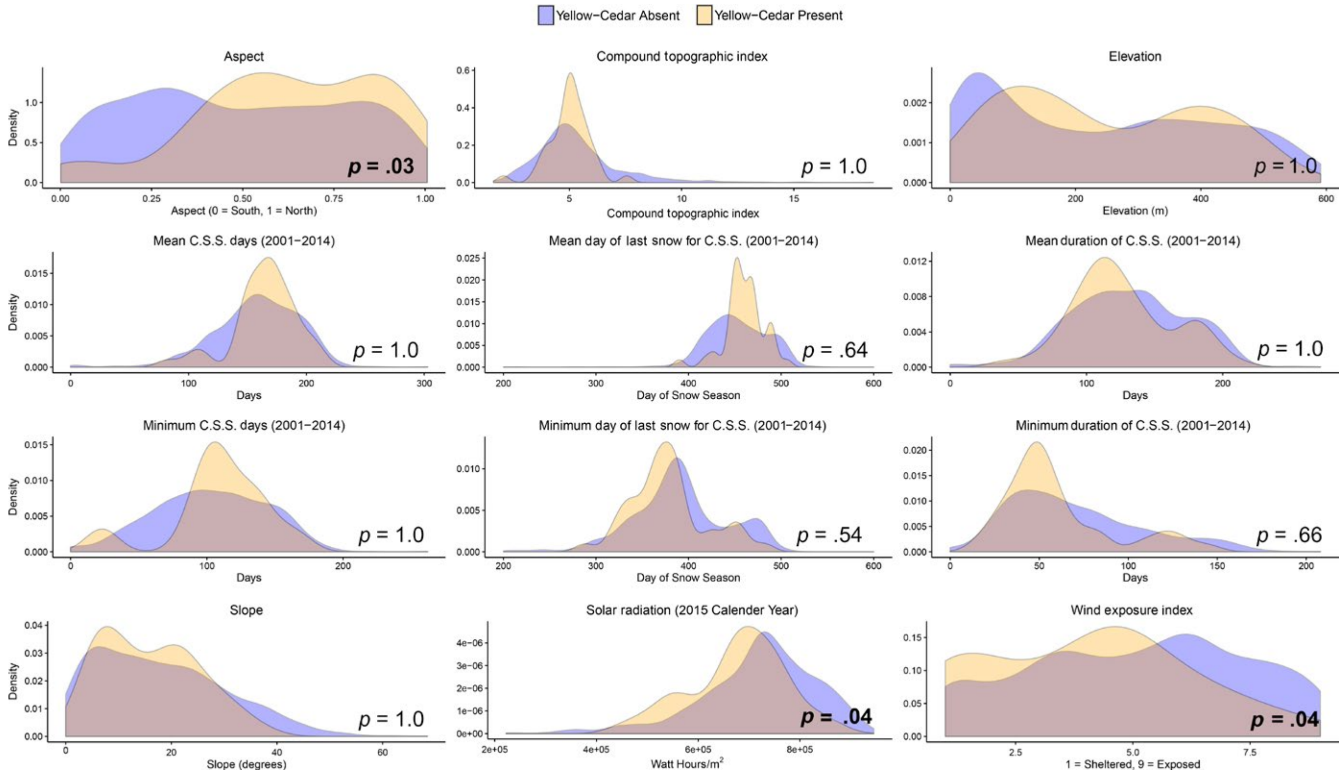

FIGURE 3 Kernel density plots comparing topographic, snow and disturbance variables for yellow-cedar occurrences and 1,000 null points. Holm/Bonferroni-adjusted Kruskal–Wallis rank-sum test *p*-values in lower right hand corner of each plot; bold indicates significant value ($\alpha = 0.05$). C.S.S., "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)

0.04 ha stand with only nine canopy dominants and limited regeneration (see "LC" and "RS" in Figure 1 and Table S1 in Appendix S1). In three fully stem mapped stands and 29 randomly distributed stand edge plots from a companion study on yellow-cedar stand development and spread into existing forests (Krapek & Buma, in revision), only 1.1% of co-dominant and dominant canopy status yellow-cedar trees were dead, while >97% of trees had fully healthy crowns (75–100% live canopy foliage), indicating limited natural senescence across stands. Within 29 stand edge plots measuring yellow-cedar regeneration and spread into currently unoccupied forests, we found ~200-year-old canopy yellow-cedar trees located abruptly at boundaries, indicating that stands were actively expanding into unoccupied habitat up until the end of the LIA. Furthermore, we found very few seedlings (13 per ha) surviving to maturity outside of stand boundaries and a mean seedling dispersal distance of only 4.65 m into unoccupied forests (Krapek & Buma, in revision). In other words, stands currently appear in a period of relative stasis with a past pulse of expansion during the LIA.

3.3 | Yellow-cedar landscape distribution

Yellow-cedar occurrences tended strongly towards north-facing slopes ($p = .03$) compared to random null points, which were distributed evenly across all aspects (Figure 3). Solar radiation ($p = .04$) and wind exposure ($p = .04$) were also significantly different for yellow-cedar occurrences (Figure 3), related to yellow-cedar's prevalence on north-facing slopes which receive less solar radiation and are sheltered from prevailing south, south-east storm winds (Buma & 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 ($p > .05$; see Fig. S1 in Appendix S2), nor did elevation, slope and CTI (Figure 3; $p > .05$).

3.4 | Habitat modelling

3.4.1 | Intersection method

The modelling approach in which we identified all areas of the landscape that fell within the same range of landscape values as the yellow-cedar occurrences (i.e., fell within the same range of slope values, and also aspect values and also snow cover values) suggests a substantial amount of potential habitat in the study area (37,797 ha of suitable habitat of 48,456 forested ha; Figure 4a). Areas not considered potential habitat using this methodology included only low elevations (no yellow-cedar occurred <28 m), and pixels at the extremes (very high or low) of snow cover variables, compound topographic index, slope and solar radiation. Despite their strong tendency towards north-facing slopes, yellow-cedar occurred across all aspects

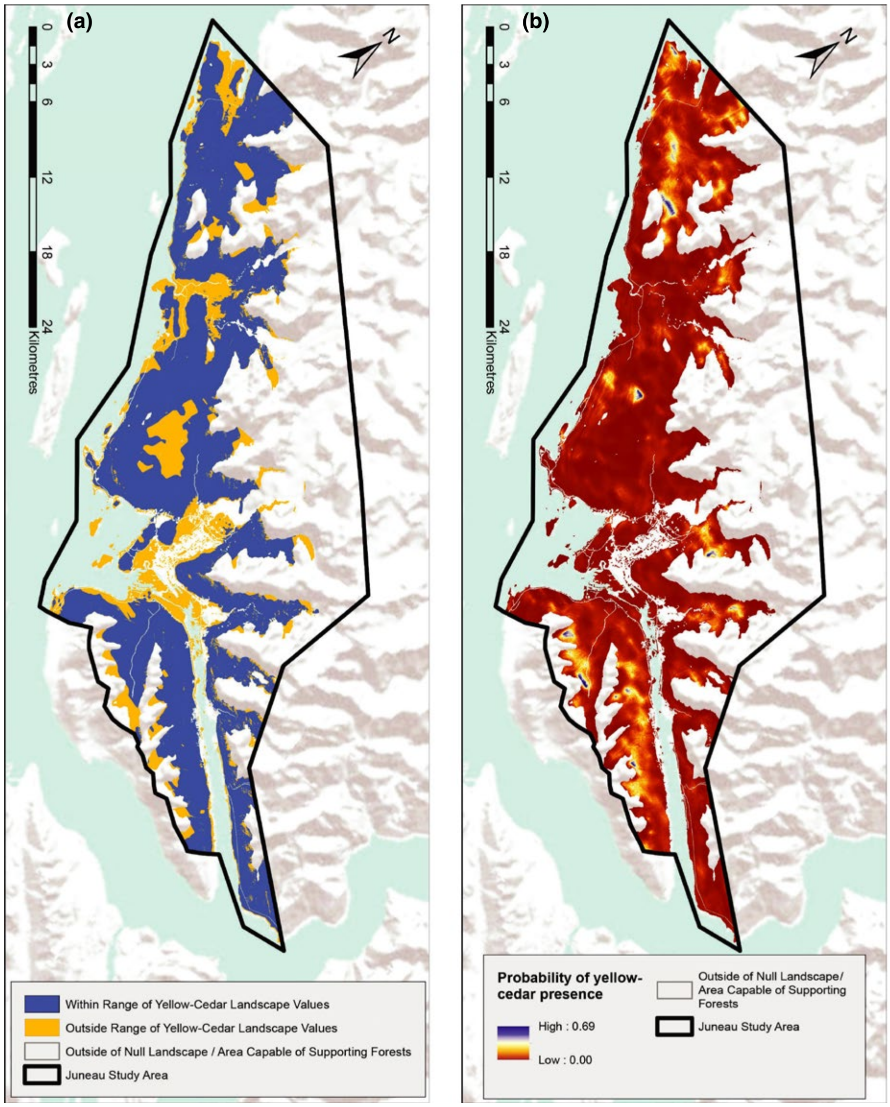

FIGURE 4 Habitat modelling. (a) Potential yellow-cedar habitat in study area based on current landscape areas known to support yellow-cedar. (b) Likelihood of yellow-cedar habitat based on generalized logistic regression model of mean landscape values for 41 yellow-cedar occurrences in study area

and wind exposure values; therefore, these variables were not useful for excluding potential habitat with this method.

3.4.2 | Generalized logistic regression

The GLM highlighted snowy, north-facing slopes with moderate CTI values throughout the study area as having a high likelihood of suitable yellow-cedar habitat (Figure 4b). Steep slopes and locations with an extremely high CTI (perennially saturated) are identified as having a very low likelihood of yellow-cedar occurrence. Of the thirteen landscape variables used in the GLM, only three were significant ($\alpha = 0.05$), all related to snow: the minimum number of total CSS days (i.e., all CSS segments with 14 days or longer snow cover totalled together; $p = .005$), the mean day of last spring snow ($p = .002$) and the duration of the CSS season (i.e., length of the longest CSS snow season segment; $p = .02$). The residual deviance of the model was 311 on 1,029 residual degrees of freedom.

Similar to the intersection method described above, the GLM suggests that yellow-cedar is not filling its potential habitat. Yellow-cedar is currently growing in areas identified by the GLM model as having a 0.01 probability of occurrence or greater (Figure 4b). The median GLM value where yellow-cedar occurs was 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 likely habitat within the study area.

3.5 | Vulnerability analysis

Study area yellow-cedar stands may become vulnerable to climatic conditions known to lead to mortality only under the high emissions (RCP 8.5) scenario examined (Figure 5). In the bidecadal period centred 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, while only the two highest elevation stands (>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 maintain a mean winter temperature below 0°C, indicating a snowpack

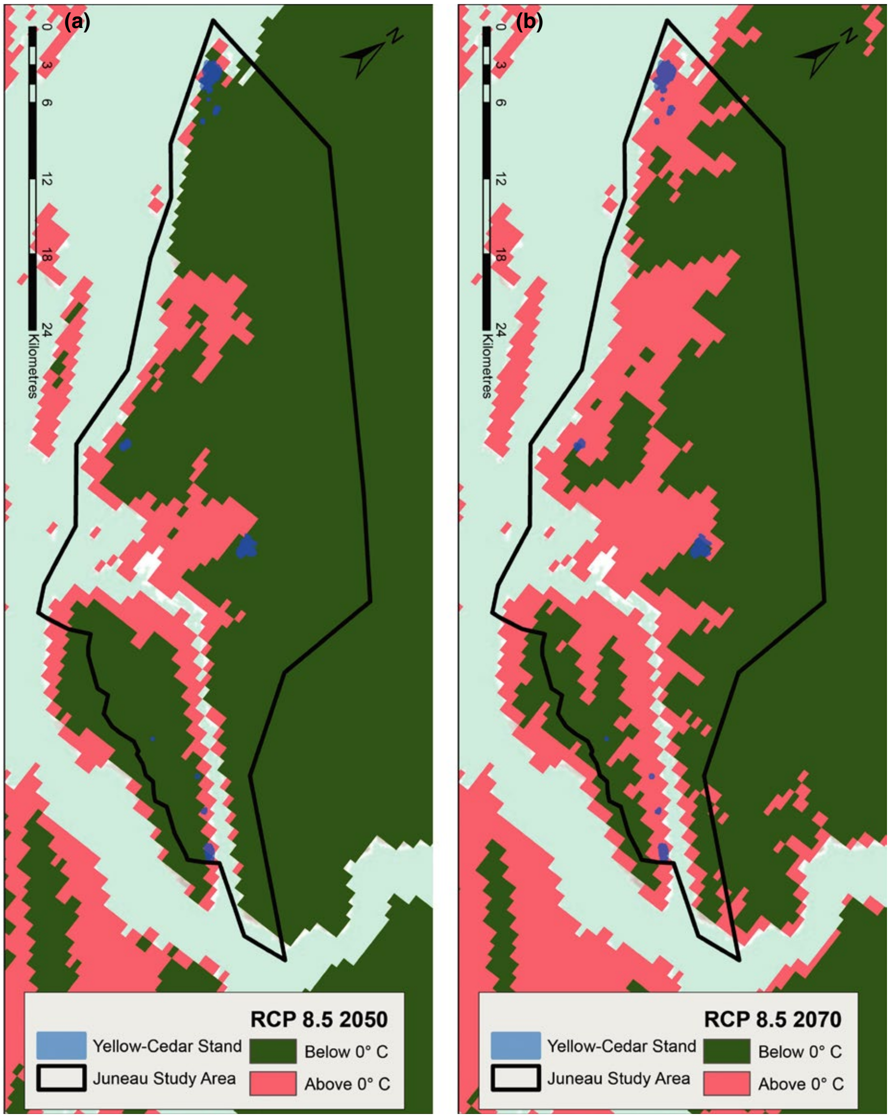

FIGURE 5 Vulnerability analysis. (a) Study area yellow-cedar stands overlaid with mean winter temperature data from the WorldClim HadGEM2-ES RCP 8.5 high emissions scenario in 2050. Note that two low-elevation stands lie within the "Above 0°C" mean winter temperature band, indicating potential vulnerability to low snow conditions. (b) Study area yellow-cedar stands 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 stands, and portions of a third, maintain a mean winter temperature conducive to a continuous winter snow regime, while all other stands become vulnerable. In the HadGEM2-ES RCP 2.6 low emissions scenario (not shown), all stands remain in the snowy "Below 0°C" band through 2070

would likely persist when yellow-cedar roots need protection from freezing events.

4 | DISCUSSION

4.1 | Yellow-cedar occurrence mapping, tree ages and stand dynamics

Our mapping confirms that there are substantial areas of unoccupied potential habitat along yellow-cedar's sparsely distributed northeastern range edge suitable for continued migration. Tree ages indicate that stands are relatively young (median age = 232 years) compared to the average (500–750 years) and maximum (>1,000 years) ages reported for mature yellow-cedar (Hennon et al., 2016; Laroque & Smith, 1999). We found an extremely low incidence (1.1%) of dead canopy status yellow-cedar trees across these leading edge stands (Krapek & Buma, in revision). Because yellow-cedar trees are extremely decay resistant, they can stand dead for up to 100 years or persist for decades on the forest floor following bole breakage (Hennon et al., 2016). If past establishment had occurred, we would expect to find evidence of large dead yellow-cedar trees on the landscape and a higher incidence of natural senescence. Instead, we find young, healthy canopy trees and limited mortality, indicating that these stands have only recently established at the front of a directional migration.

Eight of ten stands likely established and spread to their current extents during the LIA (1100–1850), a period cooler and potentially snowier than today (Wiles et al., 2014). This finding is consistent with observations by Hennon, Shaw, and Hansen (1990) and Beier, Sink, Hennon, D'Amore, and Juday (2008) that most living, mature yellow-cedar trees in southeast Alaska regenerated and grew to canopy status during the LIA. Farther south and west in the range, yellow-cedar occupies more of its potential landscape niche where the species has likely been present longer (Martin et al., 1995; Buma et al., 2016).

Although stands are relatively young and for this reason dispersal appears to be ongoing, new population establishment and range expansion are currently limited. Approximately 200-year-old yellow-cedar trees are located abruptly at stand boundaries, with few seedlings surviving to maturity in adjacent forests (Krapek & Buma, in revision). Stands appear to have been actively spreading up until the end of the LIA (ca. 1850), with little expansion or colonization over the past two centuries. Although we believe we located all yellow-cedar occurrences in the study area, confirmed by our helicopter survey and field sampling, it is possible other trees exist in relatively underexplored areas.

In total, yellow-cedar has taken >675 years to occupy 286 ha of the 37,797 ha, or <0.8%, of potentially available habitat within the study area. The species' 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. Ungulate browse may also limit yellow-cedar spread, particularly in areas of low snow accumulation (Hennon et al., 2016).

In time periods unfavourable for dispersal, yellow-cedar's longevity, tolerance of stress conditions, ability to regenerate vegetatively and high relative survivorship compared to sympatric forest trees (Hille Ris Lambers et al., 2015; Lertzman, 1995) may allow it to persist on the landscape, ultimately leading to a punctuated and relatively slow migration following the LGM. Preliminary molecular DNA work from yellow-cedar foliage collections across its range suggests that Alaska populations were founded by diverse sources and expanded at an exponential rate at some point in the past, perhaps during the LIA (Hennon et al., 2016). With a return to cooler and snowier conditions at some point in the future, yellow-cedar could experience another pulse of successful regeneration and establishment; however, this appears unlikely given projected climate scenarios (Shanley et al., 2015).

4.2 | 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 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, which generally retain more snow in the winter, potentially serving as protection from ungulate browse (Hennon et al., 2016) and from late season soil freezing events (Schaberg et al., 2011). Although none of the MODIS snow variables was significantly different between yellow-cedar occurrences and null points, the entire north-east range edge may be snowy enough for yellow-cedar, particularly during times of past establishment. Further, the MODIS record used only spans 2000–2014, a locally snowy period (NOAA, 2016), and is spatially coarse (500 m resolution) potentially obscuring longer-term trends of yellow-cedar favouring snowy locations.

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 (Martin et al., 1995). However, stands are located in wind-sheltered areas and cores from co-dominant species (*n* = 20; unpublished data) indicate that yellow-cedar is surrounded by older western and mountain hemlock and Sitka spruce, consistent with similar observations at disjunct north-western populations in Prince William Sound, Alaska (Hennon & Trummer, 2001). Therefore, yellow-cedar appears to have invaded existing forest communities during the LIA, potentially through small canopy gaps.

4.3 | Habitat modelling

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. In the first approach, we included all landscape values where yellow-cedar currently occurs as potential habitat. This treatment is likely generous because it does not account for biotic factors such as yellow-cedar's reproductive capacity, dispersal and competition with other species. However, this intersection method illustrates that large portions of the landscape are topographically and climatically similar to areas currently supporting yellow-cedar.

In contrast, the GLM approach is conservative and likely underpredicts suitable habitat due to yellow-cedar's lagged migration. Although the GLM identified moderately wet, north-facing slopes as high probability habitat, consistent with yellow-cedar's niche in the region (Hennon et al., 1990), it generally gave low probability values to the entire landscape, even locations where yellow-cedar was present. This can result from two possibilities. The first is that variables important to the distribution of yellow-cedar were not included in the model. However, the variables used encompassed the known autecology of the species (Hennon et al., 2016). The alternate hypothesis is that the species is not occupying suitable habitat within the region, and "absence" points in the model are therefore not distinct from presence points (because they are also suitable but not yet colonized). By marking absence points as non-habitat, a basic assumption in many distribution modelling methods, the GLM approach effectively forces potentially suitable landscapes to be unsuitable (Phillips & Elith, 2013; Phillips et al., 2009). More generally, this implies that for species not currently at climatic equilibrium, absence points (or pseudo-absence points in presence-only datasets) are problematic tools (Gallien, Douzet, Pratte, Zimmermann, & Thuiller, 2012). Given the predicted rapid climate changes and the comparatively slower response of species distributions, this difficulty will only become more pronounced.

The suitability of the general landscape for yellow-cedar growth is empirically demonstrated best by experimental plantings. A common garden planting established in 2010 on a former clearcut, and area of high snow accumulation within the study area is growing well with high seedling survivorship (P. E. Hennon, unpublished data). Another trial planting near Yakutat, Alaska, 300 km north-west of the study area is also thriving, well-ahead of the contiguous yellow-cedar range edge (Hennon et al., 2016). These two plantings provide evidence that yellow-cedar is perfectly adapted to grow within large areas of potential habitat outside of its current range but that competition, ungulate browse, limited dispersal capacity or other factors have been limiting active yellow-cedar range expansion since the end of the LIA.

4.4 | Vulnerability analysis

Substantial areas of yellow-cedar mortality have been observed only 100 km south of the study area (Dubois & Burr, 2015), and mortality has been progressively emerging farther north in recent decades (Hennon et al., 2016). Although large expanses of habitat within the study area are currently suitable for yellow-cedar, areas of low snow accumulation may become unsuitable in the near future. Low-elevation stands, in particular, are likely to become vulnerable to decline as regional snowpacks are rapidly diminished (Shanley et al., 2015), while only the two highest elevation stands are likely to remain snowy to 2070 in the high emissions scenario considered.

Soil drainage, which is known to be the other leading risk factor for yellow-cedar decline due to its influence on rooting depth (Hennon et al., 2012), was not considered in our vulnerability assessment. Modelling efforts which incorporate soil drainage, actual snow forecasts (rather than temperature only), and examine additional potential climate scenarios, as well as longer time-scales, are necessary to better predict the vulnerability of yellow-cedar in the future (see Hennon et al., 2016).

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 culturally and economically unique species (Hennon et al., 2016). Based on the fact that yellow-cedar has taken >675 years to occupy only 286 ha of 37,797 ha, or <0.8%, of land capable of supporting yellow-cedar forests within the study area, and because of its currently low reproductive capacity and future projected climate threats, assisted migration may be a warranted management consideration for yellow-cedar (Mueller & Hellmann, 2008). Facilitating yellow-cedar's migration north, with proper planning and monitoring, may be of low risk because of the relatively homogeneous old-growth forest conditions across southeast Alaska (Alaback, 1982; Neiland, 1971), yellow-cedar's absence from some forests ahead of its range despite apparent habitat (Martin et al., 1995), and disjunct populations currently thriving 500 km north-west of the current contiguous range edge (Hennon & Trummer, 2001). However, introduction to novel vegetation types or communities already at risk from climate change (e.g., alpine areas) should be avoided.

4.5 | Understanding species' capacity to migrate

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 favourable (Lazarus & McGill, 2014). Yellow-cedar's currently limited migration highlights that species ranges often do not respond linearly to gradually shifting mean abiotic conditions. Instead, long temporal windows which encompass episodic recruitment dynamics may be necessary when trying to predict how long-lived, woody species ranges will ultimately shift (Jackson et al., 2009; Franklin et al., 2016).

Although climate just beyond a range edge may become suitable for growth, factors such as competition (Ibáñez, Clark, & Dietze, 2009) and limited dispersal and regeneration capacity (Walck, Hidayati, Dixon, Thompson, & Poschlod, 2011) may prevent a smooth range response to changing climate. Successful colonization of new habitat may be tied to specific ecological thresholds crossed (Jackson et al., 2009), as appears to be the case for yellow-cedar and its apparent multiple colonization events during the snowier LIA climate period. Other species' past colonization of new habitats has also been attributed to episodic climatic events. In the arid Intermountain West of North America, decadal wet periods favoured range expansion of pinyon pine (*Pinus edulis* Englm.; Gray, Betancourt, Jackson, & Eddy, 2006) and periods of fire-quiescence have been tied to recruitment pulses of ponderosa pine (*Pinus ponderosa* Laws; Brown & Wu, 2005). Tree line shifts can be similarly punctuated, with recruitment pulses during periods of favourable climate, followed by persistence of long-lived adults even when recruitment is failing (Kullman, 1993; Lloyd, 2005).

As many species' leading and trailing edges converge under changing climate, detailed assessments of future migration capacity are necessary (Franklin et al., 2016). Past windows of expansion at a leading edge are the closest proxy we have for predicting future migration capacity, particularly for species currently lagging behind climatic equilibrium (Johnstone & Chapin, 2003). Precise delineations of range edge population expansion and timing of establishment are required for accurate future determinations of migration, particularly for species that must migrate through intact, undisturbed old-growth forest conditions.

5 | CONCLUSIONS

Our findings on the relatively young age of yellow-cedar stands located within the study area and large area of unoccupied potential habitat support previous hypotheses that yellow-cedar is undergoing a continued, but punctuated natural range expansion in southeast Alaska, lagging behind suitable climate conditions. Yellow-cedar has taken >675 years to occupy only 286 ha of 37,797 ha, or <0.8%, of its fundamental landscape niche in the study area. 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 favourable climate or forest composition to reproduce, leading to a pulsed migration following the LGM with a past wave of expansion during the LIA. Yellow-cedar's punctuated migration, partial occupancy of 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 economically and culturally valuable tree.

The episodic and currently limited dispersal of yellow-cedar near its leading range edge may serve as a case study for other long-lived, conifers that are failing to migrate in response to gradually shifting abiotic conditions in a warming climate. Even if ameliorating climate may favour growth in new landscapes, other factors such as competition, predation and poor dispersal ability may limit species spread. When trying to predict future ranges, we need to consider these factors, as well as longer temporal scales that may capture episodic, threshold-related dispersal dynamics. On-the-ground delineations of a species' recent range edge migration history may provide the clearest window into future dispersal capacity.

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DATA ACCESSIBILITY

Yellow-cedar occurrence geospatial data are available from the authors upon request. The IfSAR DEM data are available at: http://ifsar.gina.alaska.edu/. Snow data are available at: http://www.gina.alaska.edu/projects/modis-derived-snow-metrics. National Land Cover Database information is available at: http://www.mrlc.gov/.

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BIOSKETCH

John Krapek is a research assistant at the University of Alaska Southeast studying yellow-cedar ecology, distribution and management. Collectively, the authors have been working to understand yellow-cedar decline and ecology in southeast Alaska since the 1980s. A current focus of our research is to examine yellow-cedar's future distribution and vulnerability to climate at a range-wide perspective (i.e., from northern California to British Columbia to Alaska), and what the decline of one species on the landscape means for the future of the forest.

Author contributions: B.B., P.E.H., D.V.D. and J.K. conceived the study. J.K. and B.B. collected and analysed the data. J.K. led the writing with contributions from all authors.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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