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ARTICLE

No evidence of recent (1995–2013) decrease of yellow-cedar in Alaska

T.M. Barrett and R.R. Pattison

Abstract: Climate change is expected to impact forests worldwide, and yellow-cedar (*Callitropsis nootkatensis* (D. Don) Oerst. ex D.P. Little) decline has been used as an example of how changing climate can impact a tree species. However, most previous research has not placed yellow-cedar decline within the context of yellow-cedar overall. We used a 2004–2013 regional inventory of the temperate rainforest of Alaska (671 plots with yellow-cedar) to estimate current attributes and a subset of 564 remeasured plots (established 1995–1998) to estimate recent change. Results show that in unmanaged forests, yellow-cedar live tree basal area recently (1995–1998 to 2004–2013) increased, with a 95% confidence interval of a 0.3% to 3.3% increase per decade. Yellow-cedar has a relatively low mortality rate, 0.41% of trees per year. An analysis of live tree to snag ratios was consistent with elevated mortality of yellow-cedar prior to 1995 but also indicated that little range contraction had occurred. The large numbers and wide geographic range of yellow-cedar trees in Alaska and the recent (1995–2013) stability in the monitored population serve as important contextual information for yellow-cedar decline. This research also illustrates that understanding the spatial and temporal complexities of how tree species respond to climate change will be improved if focused studies are accompanied by regional monitoring.

Key words: forest decline, forest monitoring, climate change, *Callitropsis nootkatensis*.

Résumé : Le changement climatique devrait avoir un impact sur les forêts partout dans le monde et le dépérissement du faux-cyprès de Nootka (*Callitropsis nootkatensis* (D. Don) Oerst. ex D.P. Little) a été utilisé comme exemple pour montrer de quelle façon la modification du climat peut avoir un impact sur une espèce d'arbre. Cependant, la plupart des travaux de recherche antérieurs n'ont pas considéré le dépérissement du faux-cyprès de Nootka dans le contexte global de cette essence. Nous avons utilisé un inventaire régional couvrant les années 2004 à 2013 de la forêt humide tempérée de l'Alaska (671 places échantillons contenant du faux-cyprès de Nootka) pour estimer les attributs courants et un sous-ensemble de 564 places échantillons remesurées (établies en 1995–1998) pour évaluer les changements récents. Les résultats montrent que la surface terrière des tiges vivantes de faux-cyprès de Nootka a récemment (1995–1998 à 2004–2013) augmenté dans les forêts non aménagée avec un intervalle de confiance de la moyenne de 0,3 à 3,3 % par décennie au seuil de 95 %. Le faux-cyprès de Nootka avait un taux de mortalité relativement faible, soit 0,41 % par année. Le résultat d'une analyse du rapport entre les arbres vivants et les chicots était consistant avec une mortalité élevée du faux-cyprès de Nootka avant 1995, mais indiquait également que son aire de répartition avait peu rétréci. Le grand nombre et la vaste répartition géographique du faux-cyprès de Nootka en Alaska ainsi que la récente (1995–2013) stabilité dans la population sous surveillance constituent une information contextuelle importante au sujet du dépérissement du faux-cyprès de Nootka. Cette recherche montre aussi que la compréhension des complexités spatiale et temporelle dans la façon dont les espèces d'arbres réagissent au changement climatique sera meilleure si des études ciblées sont accompagnées d'un suivi régional. [Traduit par la Rédaction]

Mots-clés : dépérissement des forêts, surveillance des forêts, changement climatique, *Callitropsis nootkatensis*, faux-cyprès de Nootka.

1. Introduction

Climate change is expected to have a substantial impact on forests, both directly through changes in temperature and precipitation (Iverson and Prasad 2001) and indirectly through altered disturbance regimes (Dale et al. 2001). However, the nature, timing, and degree of change are very uncertain given the complexity of forest ecosystems and the limitations of climate predictions. Because yellow-cedar (*Callitropsis nootkatensis* (D. Don) Oerst. ex D.P. Little) syn. *Chamaecyparis nootkatensis*) decline provides a contemporary case of a tree species believed to have been negatively affected by warming climate (Hennon et al. 2012), it has been used as an example in research syntheses about how forest ecosystems may respond to climate change (see Allen et al. 2010; Vose et al. 2012; Wolken et al. 2011).

There is an extensive body of research about yellow-cedar decline in Alaska (e.g., see references in Hennon et al. 2016) and its links to climate change. However, most previous research does not place the decline phenomenon within the context of the overall yellow-cedar population in Alaska. In this paper, we use a comprehensive inventory of forests of southeastern Alaska to provide information on forests within the mapped area of decline, along with characteristics for the overall yellow-cedar population in Alaska.

Yellow-cedar decline is recognized as the long term (since the late 1800s) mortality of yellow-cedar trees in coastal Alaska that is

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caused by freezing damage to roots. Mortality typically occurs in yellow-cedar stands that are on poorly drained soils where roots are near the soil surface and at lower elevations where there is less snow accumulation. Yellow-cedar decline is linked to late winter – early spring warming events that are followed by extended freezing temperatures (Beier et al. 2008). Yellow-cedar undergoes dehardening of its roots during warming periods that leave roots susceptible to freezing events (Schaberg et al. 2005, 2008, 2011; D'Amore and Hennon 2006; Hennon et al. 2016).

A forest "decline" as used in forest health has a meaning somewhat different from the common interpretation of "decline" as a synonym for "decrease". A decline is characterized by a gradual loss of tree vigor followed by mortality, where causes are unknown or caused by complex relationships between abiotic and biotic factors (Manion and Lachance 1992). Another example of tree decline similar to yellow-cedar decline is the decline of yellow birch (*Betula alleghaniensis* Britt.) in northeastern North America (Bourque et al. 2005; Beier et al. 2008). The decline of yellow birch is attributed to several factors, including that it is typically shallow-rooted and is sensitive to winter thaw events that reduce cold hardiness of both roots and stems (Bourque et al. 2005).

Both yellow-cedar and yellow birch declines are consistent with a widely recognized impact of climate change on ecosystems where snow cover is common during the winter. As air temperatures warm and snow cover declines, either in amount or duration, plants are at increased risk of freezing damage (Groffman et al. 2001). In addition to trees (Groffman et al. 2001), alpine and tundra shrubs (Wipf and Rixen 2010; Gerdol et al. 2013; Wheeler et al. 2014) and wildflowers (Inouye 2008) have been shown to be susceptible to increased freezing damage. Reductions in snow can have ecosystem-level impacts such as changes in biogeochemistry, as well (Groffman et al. 2001).

Yellow-cedar decline appears to occur when the roots of yellow-cedar are exposed to cold temperatures (less than –5 °C) (Schaberg et al. 2008). Decline occurs in sites where yellow-cedar's roots are near the surface, e.g., in wet soils. Shallow rooting leaves yellow-cedar particularly susceptible to freezing events such as those that occur in areas where snowpacks have been reduced and where spring freezing events have occurred (D'Amore and Hennon 2006). Sites with wet soils also tend to have more open canopies, which increases melting of snowpacks during warming events and also increases the risk of root freezing during cold temperature events (D'Amore and Hennon 2006). Yellow-cedar trees are physiologically active early in the spring (Schaberg et al. 2005), potentially as a mechanism to capture pulses of nitrogen available in the soil (D'Amore et al. 2009). This increased activity coupled with declines in soil-insulating snowpack increase the susceptibility of yellow-cedar roots to freezing damage. Thawing events in the early springtime can increase the physiological activity and dehardening of yellow-cedar roots (Schaberg et al 2005, 2008). Winter temperatures have increased during the 20th century, which has both decreased snowpacks at lower elevations and increased the likelihood of early dehardening of yellow-cedar roots. At the same time that winter temperatures have warmed, there has not been a decrease in the occurrence of cold freezing events resulting from high-pressure arctic air influxes into the region (Beier et al. 2008). Consequently, yellow-cedar trees in low-elevation forests with wet soils are exposed to increased likelihood of freezing damage.

The estimate of approximately 200 000 ha (Hennon et al. 2012, 2016) of yellow-cedar decline in Alaska has been based on aerial survey mapping (Hennon and Wittwer 2013; Hennon et al. 2016), which consisted of annual low-altitude flights in which observers sketch-mapped the occurrence of yellow-cedar decline and other disturbances as the plane flew. Aerial surveys of tree damages are inherently challenging, particularly when assessing impacts at finer scales (Johnson and Ross 2008). Aerial surveys of yellow-cedar decline often do not detect decline in areas of low mortality and can overestimate the spatial extent of decline in areas with patchy distributions (Hennon and Wittwer 2013; Hennon et al. 2016). For example, Hennon and Wittwer (2013) found that aerial photograph interpreted data sets, which allow for finer scale assessments of decline, had only 25% of the estimated area of yellow-cedar decline compared with aerial survey efforts of the same areas.

While there has been a substantial amount of insightful research into the mechanisms underlying yellow-cedar decline, most past research has either been very localized (e.g., D'Amore and Hennon 2006) or has not used a sampling frame that would allow inference to the overall yellow-cedar population in Alaska (e.g., Hennon et al. 1990*a*; Oakes et al. 2014). Recent efforts to map the distribution of yellow-cedar in Alaska based on modelling (Ellenwood et al. 2015; Krist et al. 2014; Hennon et al. 2016) provide maps that, while potentially useful, do not provide statistically based insights into population dynamics and trends. A recently completed sample of coastal forests in Alaska by the Forest Inventory and Analysis (FIA) program of the United States (Gillespie 1999) now allows us to put research on yellow-cedar decline into context by providing estimates for the yellow-cedar population in Alaska, including both live trees and snags, using a design-based sample of Alaska's forests. Moreover, a remeasured subsample of these plots allows us to assess current dynamics for yellow-cedar for more than half of its range in Alaska. Our objective is to use this new forest inventory data to provide insights into the recent status and trends for the population of yellow-cedar trees in Alaska.

2. Methods

2.1. Data for current population estimates

Our 13.4 million ha study area (Fig. 1) was bounded by the Coastal Rainforests Level 2 ecoregion as mapped by Nowacki et al. (2001). For estimates of the current yellow-cedar population, we used 2004–2013 FIA data from plots that fell within the ecoregion. The inventory included all land with the exception of Glacier Bay National Park, which contained approximately 194 000 ha of forest (Boggs et al. 2008) or 1.4% of total forest within the study area. Plot layout consisted of four 7.3 m radius subplots that were used to select the live trees and snags with diameter at breast height (dbh; breast height = 1.37 m above the ground) of at least 12.7 cm. Live trees less than 12.7 cm dbh in the inventory were selected using four 2.1 m radius microplots, one located within each subplot. Trees were considered live if they had any living parts (leaves, buds, cambium) at or above breast height; yellow-cedar decline can result in severely damaged trees with small crowns that persist for years (Hennon et al. 1990*b*) but we did not evaluate damage in this study.

Sampling used a spatially balanced design, with a tessellation of hexagons covering the entire region and one sample plot selected per hexagon. Sampling intensity was one plot per 2419 ha, but field measurements were only taken at sample plots that intersected forest. Outside of national forest wilderness, 10% of the plots were randomly sampled without replacement for annual measurements each year from 2004 to 2013. Within national forest wilderness, measurements were only taken in 2005, resulting in a sparse (one-tenth intensity) sample. None of the plots installed in the Prince William Sound (PWS) region contained yellow-cedar trees, a reflection of both the relatively small number of yellow-cedar trees in the disjunct PWS population (Fig. 1) and the sparser sample in national forest wilderness. Sample size and other characteristics of our data set are shown in Table 1. Detailed information on methods, including how field crews determined "stand age" and "forest type", can be found in the field manuals for the inventories (USDA Forest Service 2016). Addi-

Fig. 1. The study area (green shaded area) was bounded by the Coastal Rainforests Level 2 ecoregion as mapped by Nowacki et al. (2001). Viereck and Little's (2007) range map for yellow-cedar depicts the approximate location of the primary population in Southeast Alaska (light blue polygon, right) and the small disjunct population in Prince William Sound (light blue polygon, left).

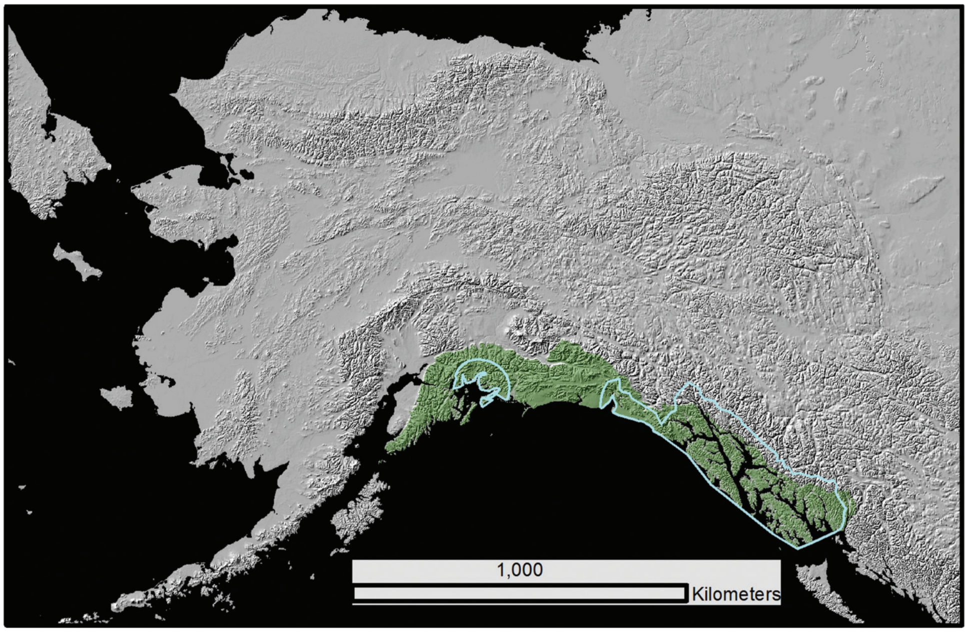

Table 1. Data used for current population estimates and estimates of change.

	Data for current population estimates (2004–2013 inventory)	Remeasurement data (1995–2003 and 2004–2013)
Total population sampled		
Land area (million ha)	13.39	10.05
Sample size (plots)	5536	3890
Forested plots	1790	1389
Plots with yellow-cedar trees	671	564
Live trees measured (≥2.5 cm dbh)	56 189	43 187
Live yellow-cedar trees measured (≥2.5 cm dbh)	7975	6242
Yellow-cedar snags measured (≥12.7 cm dbh)	2803	NA
Population within mapped area of yellow-cedar decline		
Land area (million ha)	0.23	0.14
Sample size (plots)	84	57
Forested plots	63	55
Plots with yellow-cedar trees	48	42
Live trees measured (≥2.5 cm dbh)	2516	2048
Live yellow-cedar trees measured (≥2.5 cm dbh)	722	562
Yellow-cedar snags measured (≥12.7 cm dbh)	338	NA

Note: The land area that the samples are drawn from differs because the 1995–2003 inventory did not include national forest wilderness. Glacier Bay National Park is excluded from both inventories.

tional information on data availability and limitations is shown in the Supplemental material[1].

2.2. Data for estimates of change

The analysis of change used a subset of the 2004–2013 plots (Table 1) that had repeat measurements from an earlier 1995–2003 inventory. This remeasurement data set was a sample from all land with the exception of national forest wilderness (which was not sampled in 1995–2003) and Glacier Bay National Park (GBNP). If we use Oakes et al.'s (2015) estimate of 16 120 ha of forest with yellow-cedar in GBNP, this would mean that the remeasurement estimates apply to about 65% of the estimated 2 354 000 forested ha in Alaska with yellow-cedar trees.

Sampling intensity for the remeasurement data set was one plot per 2420 ha (Table 1). Because the 1995–2003 inventory was installed starting in the southeast and moving westward along the Gulf of Alaska, plots with yellow-cedar trees were first measured between 1995 and 1998, resulting in a remeasurement period ranging from 6 to 18 years, with a mean interval of 12.2 years. For estimated rates of net change, individual observations at each sampling unit (a plot) were converted to annual values by dividing observed change by the number of years between measurements. For example, a plot with a net change in live tree basal area of 10 $m^2 \cdot ha^{-1}$ from 1995 to 2010 would be treated as an observation of annual net change of 0.67 $m^2 \cdot ha^{-1} \cdot year^{-1}$.

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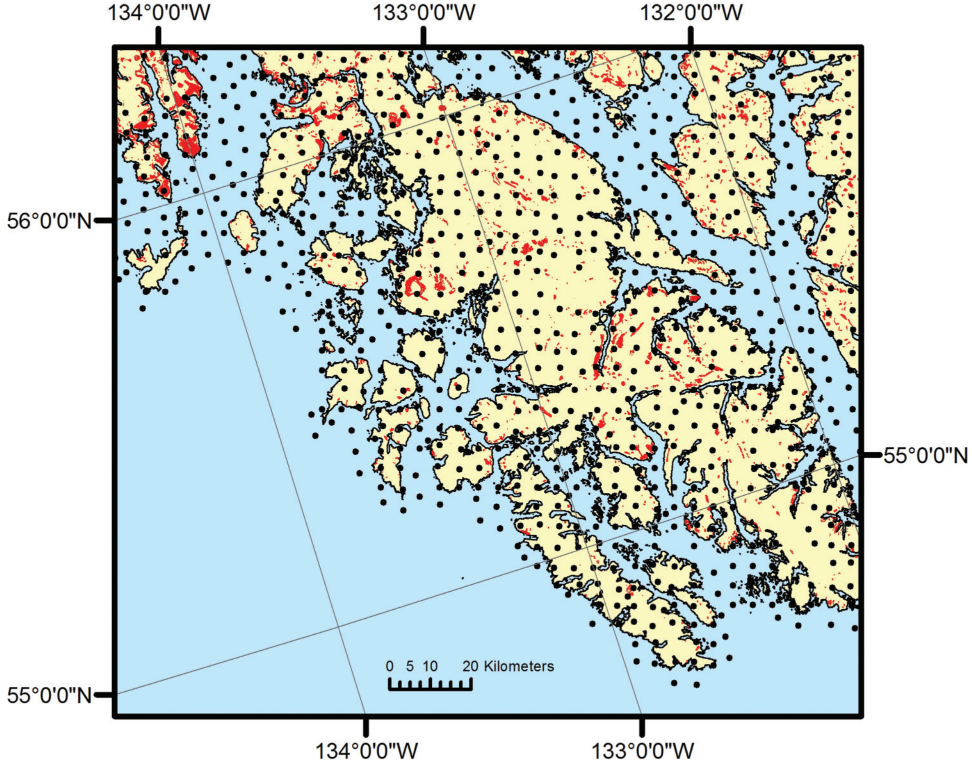
[1] Supplemental material is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2016-0335.

Fig. 2. A portion of the study area around Prince of Wales Island, Alaska. Points indicate approximate locations of field plots. GIS data for the mapped area of yellow-cedar decline (shown in red) was obtained from the USDA Forest Service Alaska Region Forest Health Protection office in Juneau, Alaska, on 5 May 2015.



A mortality tree was defined as a tree that was live at the first inventory with at least 12.7 cm dbh but dead at the second inventory; any live branch above breast height was sufficient for a tree to be considered live. Mortality rate estimates were converted to annual rates assuming compounded mortality (Larson and Franklin 2010). The location of the microplot used to measure small live trees (dbh < 12.7 cm) was changed between the inventories, preventing estimates of growth or mortality for small trees. A series of data-editing steps were taken to reconcile the measurements from the two inventories. For those instances in which live trees were missed at the first visit or were newly included because of procedural changes, diameters were backdated to the time of the periodic inventory using increment cores (1480 trees of which 227 were yellow-cedar) or models (266 trees of which 33 were yellow-cedar). Where species identifications were corrected during the second inventory, the identification at the second inventory was assumed to be correct.

The definition of "forest" shifted between the two inventories; the first inventory excluded Krumholtz forest and used a definition of forest based on canopy cover, and the second inventory included Krumholtz forest and used a definition of forest based on tree stocking. Only subplots meeting the forest definition at both time periods were used in the analysis of growth and mortality. Thus estimates of change reflect changes within the forest rather than increases or decreases of forested areas.

2.3. Analysis

We looked at the proportion of plots that had snags but not live trees as an indication of possible ongoing range contraction. Only live trees and snags greater than 12.7 cm dbh were used for this metric because standing dead trees less than 12.7 cm dbh were not included in these inventories. Basal area refers to the cross-sectional area of tree stems at 1.37 m above the ground and was calculated from field-measured tree diameters. For land ownership categories, "private" included land owned by native villages as well as Native Alaska Corporations. "Other" land ownership included state, local, and Bureau of Land Management land. Land ownership was based on the time of inventory, and thus the 2015 land transfers finalizing the Alaska Native Claims Settlement Act were not incorporated. The categories of "managed" and "unmanaged" indicated whether or not there was any record of harvesting on the plot, either prior to the first inventory or between the two inventories. Estimates of area where yellow-cedar occurs were influenced by the plot size and configuration (Gray 2003); using a coarser resolution to determine occupancy would result in larger area estimates (see Supplemental material[1]).

The State and Private Forestry Program in Alaska publishes aerial survey data on yellow-cedar decline each year as part of an annual report on forest health conditions (e.g., USDA Forest Service Alaska Region Forest Health Protection 2016) and maintains a cumulative map (spatial data set) of yellow-cedar decline developed from these aerial surveys. The cumulative map has been used by researchers (e.g., Beier et al. 2008; Hennon et al. 2012) as the basis for area estimates of how much yellow-cedar decline occurs in Alaska. We used the cumulative yellow-cedar decline map (June 2015 version) to compare the yellow-cedar population within the mapped decline area to that outside the mapped decline area (Fig. 2). Actual plot coordinates were used for analysis, and publically available coordinates were used for display. Comparisons within and outside of mapped decline areas included estimated population totals of yellow-cedar trees, live tree to snag ratios, and estimates of net change in basal area and numbers of trees.

We used the national standard FIA statistical methods (Bechtold and Patterson 2005) to calculate estimates of population totals and means. Ratio estimates (e.g., basal area per hectare) used a combined ratio estimator (Cochran 1977). Standard error (SE) esti-

Table 2. Forest area estimates (in thousand hectares, $\times 10^3$ ha) for yellow-cedar in Southeast Alaska, based on 2004–2013 FIA inventory.

							Mapped decline area			
	Total forest area in ecoregion, $\times 10^3$ ha		Forest area with yellow-cedar trees (live or snags), $\times 10^3$ ha		Forest area classified as yellow-cedar forest, $\times 10^3$ ha		Forest area, $\times 10^3$ ha		Forest area with yellow-cedar trees (live or snags), $\times 10^3$ ha	
Ownership	Area	SE	Area	SE	Area	SE	Area	SE	Area	SE
Private	456	26	87	12	33	9	13	6	11	5
Tongass National Forest	3961	91	2025	104	881	87	199	44	170	43
Designated wilderness	1501	88	755	96	368	81	84	41	82	41
Other forest	2460	38	1270	42	513	32	115	17	89	15
Other	940	69	47	10	21	7	6	4	1	2
Total	5357	94	2160	105	935	87	217	45	182	44

Note: Forest area with yellow cedar trees is based on stems greater than 12.7 cm dbh, excluding Glacier Bay National Park. Boundary for study area is based on the ecoregion map for the Alexander Archipelago, Chugach–St. Elias Mountains, and Gulf of Alaska coastal sections (Nowacki et al. 2001). The shaded rows are subsets of the Tongass National Forest and as such are not included in the Total.

mates also used the national methods and are shown in the text as ±SE. Where we interpret change as an increase or decrease, it indicates the 95% confidence interval (CI) (estimate ± 1.96 SE) did not include zero.

3. Results

3.1. Current population of yellow-cedar

We estimated that there were 2.16 million ha of forest with yellow-cedar trees in Southeast Alaska, based on the most recent (2004–2013) inventory. Yellow-cedar was the predominant species (as classified by the field crew and denoted as the "forest type") in 43% of forests with yellow-cedar trees. For forests with yellow-cedar trees, 94% of the area was within the Tongass National Forest and only 4% was privately owned (Table 2). Less than 3% of the 2 million ha of forest with yellow-cedar trees was found in managed stands, where harvest had occurred, and about 35% of forest with yellow-cedar trees was within designated wilderness areas.

Of the estimated 1.39 billion live yellow-cedar trees with dbh ≥ 2.54 cm in Alaska (Supplemental Table S1[1]), 90% were outside of the aerial survey mapped polygons of yellow-cedar decline. For stands in which yellow-cedar was predominant, about 87% of the total area within Alaska was found outside of the mapped decline polygons. Most yellow-cedar grew in old stands (Supplemental Table S2[1]). Live trees to snag ratios increased as elevation increased (Fig. 3).

Within the area of mapped decline, forest types included yellow-cedar (58% of forest area), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (28%), western redcedar (*Thuja plicata* Donn ex D. Don) (7%), shore pine (*Pinus contorta* Dougl. ex Loud. ssp. *contorta*) (5%), and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) (2%). Live tree species composition by basal area within the mapped area of decline was yellow-cedar (44%), western hemlock (35%), Sitka spruce (*Picea sitchensis* (Bong.) Carr.) (8%), western redcedar (6%), mountain hemlock (5%), and shore pine (2%). Snag composition in the decline area (by numbers of snags) was yellow-cedar (50%), hemlock (39%), Sitka spruce (7%), shore pine (2%), and western redcedar (2%).

The aerial survey did detect areas of relatively higher yellow-cedar density, both live trees and snags. In stands with yellow-cedar inside the mapped decline area, mean tree density for yellow-cedar trees ≥ 12.7 cm dbh was 132 live trees·ha^{-1} and 47 snags·ha^{-1}; outside the mapped area of decline, mean tree density for yellow-cedar trees ≥ 12.7 cm dbh was 66 live trees·ha^{-1} and 24 snags·ha^{-1}. However, the aerial survey did not appear to be successful at identifying areas where past mortality rates (live tree to snag ratios) were higher. The live tree to snag ratio for yellow-cedar trees with dbh greater than 12.7 cm was nearly identical between areas within mapped decline (2.83:1) and areas without mapped decline (2.79:1). Both inside and outside the mapped decline region, over half of stands with yellow-cedar had less than 20% of yellow-cedar basal area in snags. About 8% (or 175 000 ha) of stands with yellow-cedar had high (>70%) levels of yellow-cedar basal area in snags (Supplemental Table S3[1]).

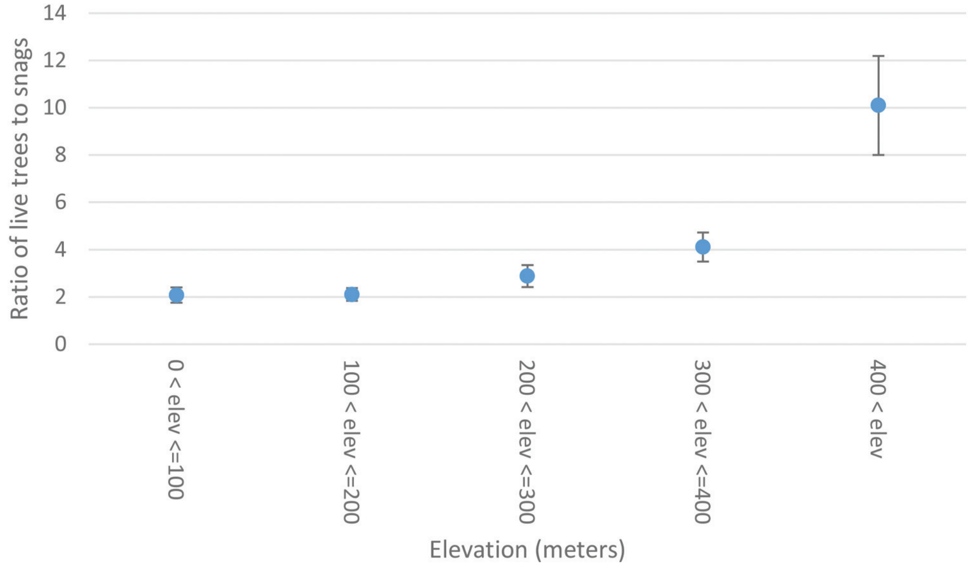
One of the important questions about yellow-cedar population dynamics is whether there is a contraction of range occurring, one indication of which would be plots with yellow-cedar snags but no live yellow-cedar trees present. Within the mapped decline area, only one of the 48 plots with yellow-cedar had snags but no live yellow-cedar trees with dbh > 12.7 cm; outside the mapped decline area, 20 of 623 plots with yellow-cedar had snags but no live yellow-cedar trees. Absence of live trees where snags were present could have indicated an area in which yellow-cedar had died off. It also could have occurred by chance when there were live trees present in the surrounding stand, given the small footprint of the plots. For comparison, the 3.1% of plots with yellow-cedar that had yellow-cedar snags but no yellow-cedar live trees measured is within the range of the same metric calculated for other common tree species: western hemlock (1.0%); mountain hemlock (1.3%); shore pine (2.9%); western redcedar (3.0%); and Sitka spruce (4.6%).

3.2. Estimates of mortality and net change

Within the sampled area, which excluded national forest wilderness and the GBNP, the population of yellow-cedar was very stable between the two inventories; the 95% CI for change in yellow-cedar's total live tree basal area was a range of a 1.1% decrease per decade to a 2.3% increase per decade. If we separate out managed areas in which harvesting has occurred, the remaining yellow-cedar population increased, with a 95% CI of a 0.3% to 3.3% increase in live tree basal area (Table 3). Similar results indicating a slight increase in yellow-cedar on unmanaged lands held true when the metric was changed to biomass. In terms of numbers of trees, most of the increase in yellow-cedar on unmanaged lands occurred in trees less than 12.7 cm dbh (Supplemental Table S4[1]). There were roughly 384 000 ha of managed forest in which harvesting had occurred in the temperate rainforest ecoregion, with yellow-cedar found on about 15% of that land, and within that category, yellow-cedar had an estimated decrease (Table 3).

The average mortality rate for the overall yellow-cedar population was higher than the mortality rate of western redcedar but not higher than mortality rates for the other common species in the temperate rainforest ecoregion (Fig. 4). The estimated rate of mortality for yellow-cedar within the mapped decline area was 0.49% (±0.14%) per year, not significantly different from the estimated rate of mortality outside the mapped decline area (0.40% ± 0.04% per year).

Fig. 3. Ratio of live trees to snags by elevation class for yellow-cedar in Alaska, excluding Glacier Bay National Park. [This figure is available in colour online.]



4. Discussion

Given the decay resistance of yellow-cedar snags, which can remain standing for 80 to 100 years after tree death (Hennon et al. 1990*b*; Kelsey et al. 2005), the small fraction of plots with snags but no live trees present indicates that little range contraction of yellow-cedar in Alaska has occurred in recent decades. This is consistent with researchers' observations from other studies that extirpation did not appear to be occurring (Oakes et al. 2014) and that it is common to find 30% yellow-cedar survivorship even in stands with severe decline (Hennon et al. 2016).

We found that recent (1995–1998 to 2004–2013) mortality rates were lower for yellow-cedar than for most other species. Our results also show a very slight recent increase in the population of live yellow-cedar within unmanaged forest, as measured by basal area, excluding GBNP and national forest wilderness where monitoring is not conducted. The 1995–2013 stability of this part of the population contrasts with the perception, presented in a recent petition to list yellow-cedar under the Endangered Species Act, that yellow-cedar is rapidly decreasing (Center for Biological Diversity 2014). Part of the confusion about the current population dynamics may lie with the use of the term "mortality" in relation to the mapped decline area (e.g., in Hennon et al. 2006, 2012, and elsewhere), which was primarily based on observations of dead trees, some of which had died up to a century earlier (Hennon et al. 1990*b*; Kelsey et al. 2005).

While managed forest (where harvest has occurred) had an estimated decrease in yellow-cedar, the results should be interpreted cautiously; because only 3% of forest with yellow-cedar trees fell into the managed forest category, the sample size in this category was small (24 plots). We also caution against extrapolating mortality rates and net change to national forest wilderness or GBNP, as neither the wilderness areas nor the park are randomly placed on the landscape.

There is indirect evidence of a decrease in the population that occurred prior to 1995, namely the low live tree to snag ratios (2.8 to 1) that we observed for this species in Alaska. The FIA data for Oregon and Washington provide a live tree to snag ratio for yellow-cedar of 8.4 to 1 on reserved lands, which are public lands where statute or agency mandate prohibits management for wood products. Differences in disturbance regimes and rates of decay, fall down, and growth between Southeast Alaska and the Pacific Northwest argue against assuming that the ratio should be the same, but nonetheless, the very high number of yellow-cedar snags in Alaska suggests to us that it is likely that population decreases took place prior to 1995. This indirect evidence of a previous decrease in yellow-cedar corresponds with other research describing high levels of mortality that started around 1880 and became widespread by 1927 (Hennon et al. 1990*b*) and a high level of mortality from the mid-1960s to the mid-1980s (Hennon and Shaw 1994).

The indirect evidence of a past decrease combined with current stability in the monitored population suggests that even regional-level tree population responses to climate change may be temporally sporadic rather than gradual. This is consistent with Beier et al.'s (2008) conclusions that the triggering event for yellow-cedar decline — warming days followed by a protracted cold event in years with low snowpack — does not happen very often. The competitive release in surviving yellow-cedar observed by Beier et al. (2008) on decline plots may also be contributing to the slight increase in basal area that we observed, and the relatively large increase in numbers of small trees (less than 12.7 cm dbh) in our results (Supplemental Table S4[1]) suggests that high levels of regeneration have been occurring.

The increase in live tree to snag ratios as elevation increased that we observed may be a consequence of higher past (pre-1995) mortality of yellow-cedar at lower elevations, and this finding is consistent with other research describing decline as primarily occurring at lower elevations (Beier et al. 2008; Hennon and Shaw 1994). Yellow-cedar at higher elevations appear to benefit from the colder microclimate, which reduces the frequency and severity of thaw events and lessens the likelihood of premature dehardening (Beier et al. 2008). Additionally, yellow-cedar at higher elevations would typically have greater snow accumulation, which insulates roots (D'Amore and Hennon 2006). Increases in the live tree to snag ratio with increasing elevation could also indicate that yellow-cedar has been expanding into higher elevation areas, although yellow-cedar's potential for rapid migration is thought to be limited (Krapek and Buma 2015).

The mortality rate that we observed was within the range of the 0.2% annual mortality observed by Larson and Franklin (2010) and the 0.7% annual mortality observed by Edmonds et al. (1993) for yellow-cedar in old-growth forests in Washington. Larson and Franklin's (2010) average annual mortality estimate in Mount Rainier National Park for yellow-cedar trees ≥ 15 cm dbh was

Table 3. Change in mean basal area composition ($m^2 \cdot ha^{-1}$) for forests with yellow-cedar trees within the Alaskan temperate rainforest.

	Management category								
	Unmanaged (n = 540)			Managed (n = 24)			All forests (n = 564)		
Species	Initial basal area, $m^2 \cdot ha^{-1}$	Basal area change per decade, $m^2 \cdot ha^{-1}$	SE for basal area change, $m^2 \cdot ha^{-1}$	Initial basal area, $m^2 \cdot ha^{-1}$	Basal area change per decade, $m^2 \cdot ha^{-1}$	SE for basal area change, $m^2 \cdot ha^{-1}$	Initial basal area, $m^2 \cdot ha^{-1}$	Basal area change per decade, $m^2 \cdot ha^{-1}$	SE for basal area change, $m^2 \cdot ha^{-1}$
Yellow-cedar	12.81	0.23	0.10	12.10	−3.61	1.17	12.78	0.08	0.11
Shore pine	1.83	−0.05	0.04	0.61	0.02	0.06	1.78	−0.04	0.04
Mountain hemlock	5.04	−0.10	0.07	3.37	−0.47	0.71	4.97	−0.12	0.07
Sitka spruce	2.67	0.03	0.07	2.53	0.24	0.88	2.66	0.04	0.07
Western hemlock	14.81	−0.11	0.15	14.04	−3.41	1.58	14.78	−0.24	0.16
Western redcedar	5.05	0.28	0.06	3.74	−1.24	1.37	5.00	0.22	0.08
Hardwoods	0.05	−0.01	0.01	0.23	−0.21	0.38	0.06	−0.02	0.02
All species	42.26	0.28	0.22	36.61	−8.67	3.91	42.03	−0.08	0.28

Note: Management category denotes whether or not harvesting has occurred in the stand. Estimates include all live trees with >2.54 cm dbh. Areas within national forest wilderness or Glacier Bay National Park were not included.

about half of the 0.41% (±0.04%) per year mortality that we observed for yellow-cedar trees ≥ 15 cm dbh in unmanaged forest. Higher mortality rates combined with the stability of the population overall would be consistent with the hypothesis that competitive release and regeneration of yellow-cedar was substantial during the time period between the two inventories. A complex spatial and temporal pattern of dieback and recovery would also be consistent with Bourque et al.'s (2005) observations for a similar dieback of yellow-birch in eastern North America, which was also attributed to sporadic thaw–freeze events.

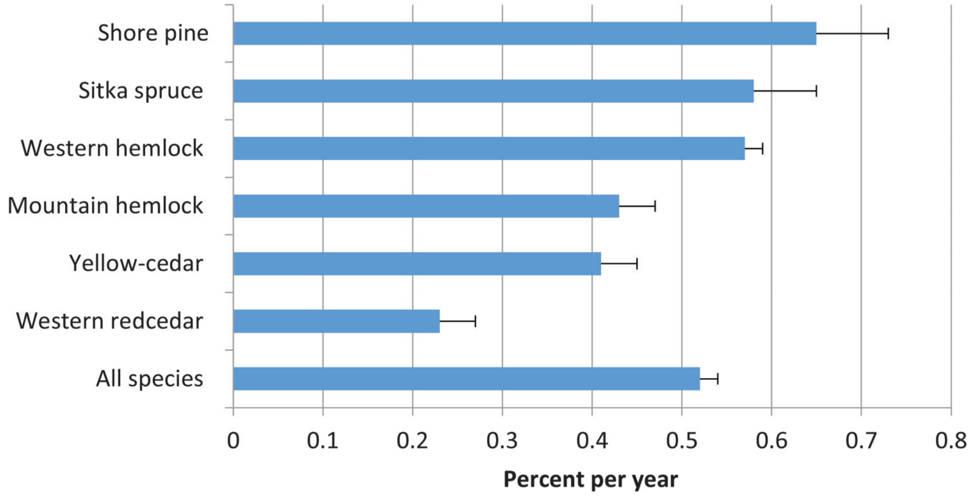
Our results do indicate that species shifts are occurring within forests where yellow-cedar is found. Oakes et al. (2014) found succession from western hemlock occurring on their study plots; our results found that among competing species, the greatest increase was in western redcedar. A recent tree ring study (Sullivan et al. 2015) indicates that shore pine, which frequently co-occurs with yellow-cedar in forests of Southeast Alaska, has had a growth decrease starting in the 1960s that is correlated with reduced diurnal temperature range and may be caused by increased infection from foliar pathogens. Because both shore pine and yellow-cedar are at the northern portion of their range in Alaska, the recent population dynamics for these two species illustrates that using simple latitudinal metrics for predicting tree species shifts in response to climate can be problematic.

Ninety percent of Alaska's yellow-cedar population (by numbers of trees) is outside the area of mapped decline. Within the area of mapped decline, 26.1% of yellow-cedar trees are snags, which is about the same as the 26.4% of yellow-cedar trees in snags found outside the mapped area of decline. Mortality rates from the remeasured plots also were similar inside and outside the mapped decline areas. One statistic used by researchers has been that there are over 200 000 ha of mapped yellow-cedar decline in Alaska in which up to 70% of yellow-cedar trees are dead (e.g., D'Amore and Hennon 2006; Hennon et al. 2012), with the 200 000 ha estimate referring to the total land area within the boundaries of the mapped yellow-cedar decline. Our research found that within the mapped decline area, just 4000 to 12 000 ha (68% CI) of forest had over 70% of yellow-cedar basal area in snags. It appears that the mapping process for yellow-cedar decline primarily distinguished areas where yellow-cedar is common rather than areas where yellow-cedar had substantially higher past or present mortality rates. This finding is consistent with Hennon and Wittwer's (2013) finding that the aerial survey overestimated area of decline by 400% compared with the more detailed aerial photograph interpreted data sets, observations that the aerial survey misses areas of mortality in stands where yellow-cedar is a minor component of species makeup (Hennon et al. 2016), and the difficulty of distinguishing live yellow-cedar from co-occurring tree species in the aerial survey (Hennon et al. 2016).

In summary, there are a number of reasons why our research results may contrast with perceptions about yellow-cedar decline. First, our study region included the entire range of yellow-cedar in Alaska (excluding the GBNP), a substantially larger region than most previous work. Second, the study's time frame (1995–2013) may have intersected with a relatively low period of decline-related mortality. Third, competitive release and regeneration of surviving yellow-cedar in stands previously affected by decline would contribute to the growth observed. Fourth, we have used a design-based sample that allows statistically based insights into yellow-cedar dynamics at the regional level; a substantial portion of previous research was focused primarily on decline-affected stands and trees. These differences provide a good illustration of the importance of using long-term regional monitoring to accompany focused studies when trying to understand the impact of changing climate on forest ecosystems.

Areas of active yellow-cedar decline have been observed by other researchers during the time period of our inventory (Hennon et al. 2016); it is likely that the larger scope of the FIA data

Fig. 4. Average annual mortality for common tree species in the Alaskan temperate rainforest for trees with dbh ≥ 12.7 cm, based on measurements from plots installed in 1995–2003 and remeasured in 2004–2013, excluding Glacier Bay National Park and national forest wilderness. [This figure is available in colour online.]



relative to these areas is a primary reason for the overall stability in estimated number of live trees that we observed. Although our results show a small recent increase in mean yellow-cedar basal area within unmanaged forests, we do not assume that this trend will continue in the future. The identified cause of yellow-cedar decline is the combination of low snowpack and freezing events in the spring (D'Amore and Hennon 2006; Hennon et al. 2016 and references therein). It is certainly possible that these conditions could continue to occur and over an expanding area as the climate in Southeast Alaska changes (Beier et al. 2008; Hennon et al. 2016). It is also possible that yellow-cedar tree numbers could show a decrease in future decades. However, the large numbers and wide range of yellow-cedar trees in Alaska, the recent increase in yellow-cedar basal area on unmanaged forest where most of the habitat occurs, and the indication that very little range contraction has occurred in past decades provide evidence against near-term extirpation and suggest that the response of tree species to changing climate can be spatially and temporally complex.

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