

Long-term vegetation changes in a temperate forest impacted by climate change

LAUREN E. OAKES,^{1,†} PAUL E. HENNON,² KEVIN L. O'HARA,³ AND RODOLFO DIRZO⁴

¹Emmett Interdisciplinary Program in Environment and Resources, Stanford University, Stanford, California 94305 USA

²Forestry Sciences Laboratory, Pacific Northwest Research Station, USDA Forest Service, Juneau, Alaska 99801 USA

³Department of Environmental Science, Policy, and Management, University of California, Berkeley, California 94720 USA

⁴Department of Biology, Stanford University, Stanford, California 94305 USA

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Abstract. Pervasive forest mortality is expected to increase in future decades as a result of increasing temperatures. Climate-induced forest dieback can have consequences on ecosystem services, potentially mediated by changes in forest structure and understory community composition that emerge in response to tree death. Although many dieback events around the world have been documented in recent years, yellow-cedar (*Callitropsis nootkatensis*) decline provides an opportunity to study vegetation changes occurring over the past century. Current research identifies climate-related reductions in snow cover as a key driver of this species dieback. To examine the process of forest development post-dieback, we conducted vegetation surveys at 50 plots along the outer coast of southeast Alaska across a chronosequence of mortality. Our main study objectives were to examine changes in seedling and sapling abundance, and community structure of conifer species in the overstory; effects of yellow-cedar mortality on plant diversity and community composition of functional groups in the understory; and volume of key forage species for Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) managed throughout the region. The probability of yellow-cedar sapling occurrence was reduced across the chronosequence. Yellow-cedar seedling and sapling abundance also decreased. We observed a turnover from yellow-cedar to western hemlock (*Tsuga heterophylla*) dominated forests. Functional plant diversity increased and the community composition of the understory changed across the chronosequence. Bryophytes became less abundant and grasses more abundant in the early stages of stand development, and shrubs increased in relative abundance in latter stages. Our results demonstrate that yellow-cedar is significantly less likely to regenerate in forests affected by widespread mortality, and a species dieback can dynamically rearrange the plant community over time. These findings emphasize the importance of considering long-term temporal dynamics when assessing the impacts of climate change on biodiversity and ecosystem services, and adapting forest management to a changing climate.

Key words: Alaska; biodiversity; *Callitropsis nootkatensis*; climate change; community composition; disturbance; forest dieback; stand development.

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† **E-mail:** leoakes@stanford.edu

INTRODUCTION

Tree death is a natural part of forest dynamics (Franklin et al. 1987), but increasing rates of mortality can result when climatic conditions

exceed a species' physiological threshold (Allen 2009). Although directional climate change has historically resulted in shifts in the distributions of species and ecosystems (Davis 1986), comparatively rapid shifts in tree distributions attributed

to anthropogenic climate change have been documented (Parmesan 2006, Lenoir et al. 2008, Harsch et al. 2009) on all six plant-covered continents (Allen and Breshears 2007, Allen et al. 2010). Recent research has focused predominantly on causal mechanisms of tree death, feedbacks to the climate system, and predictive modeling (Bonan 2008, Adams et al. 2009, Morin and Thuiller 2009, Zeppel et al. 2011). Ecologists generally agree that trees and forests in temperate regions will shift to higher latitudes and upward in elevation due to warming trends (Peters 1990, Hughes 2000, Walther et al. 2002). However, understanding how forests will behave at the “trailing ends” is limited (Matyas 2010). Stand development patterns following forest mortality events are of considerable interest because they indicate future structure and composition of affected forests, and the ability of these forests to maintain biodiversity and other ecosystem services (Dale et al. 2000, Van Mantgem et al. 2009, Daniels et al. 2011, Hennon et al. 2012). Although widespread mortality events can have negative impacts to ecosystem services (e.g., loss of economically valuable timber or cultural services, such as aesthetic value) (Anderegg et al. 2013), there may be benefits that are also important for adaptation in the human dimension (Spittlehouse 2005, Moser and Ekstrom 2010). A global overview of climate-induced forest mortality (Allen et al. 2010) provides a detailed assessment of events driven by climatic water/heat stress since 1970; few of these documented dieback events provide opportunity to examine vegetation changes that occur over a longer time frame.

Yellow-cedar (*Callitropsis nootkatensis*; D. Don; Oerst. ex D.P. Little), a species distributed from the northern Klamath Mountains of California to Prince William Sound in Alaska, has been dying in southeast Alaska since the late 1800s with intensifying rates observed in the 1970s and 1980s (Hennon and Shaw 1994). Recent research reveals a complex “tree injury pathway” where climate change plays a key role in a web of interactions leading to widespread yellow-cedar mortality, referred to as yellow-cedar decline (Hennon et al. 2012). Prominent factors in this injury pathway include cold tolerance of roots, timing of dehardening, and regional trends of reduced snowpack at low elevations (Schaberg et

al. 2005, 2008, 2011, Beier et al. 2008). Early springtime thaws trigger dehardening and reduce snow cover that insulates soil and shallow fine roots from periodic extreme cold events; this can lead to injury of yellow-cedar roots to initiate tree mortality, which is predominantly limited to lower elevations (Schaberg et al. 2005, 2008, 2011, D’Amore and Hennon 2006, Beier et al. 2008, Hennon et al. 2012). Despite the extent of research on the mechanisms of decline, overstory and understory dynamics in declining stands are not well understood (D’Amore et al. 2009).

The direct loss of yellow-cedar has important ecological, economic, and cultural implications; however, other changes are also relevant in these forests that emerge in response to decline. Researchers are just beginning to understand the influence of dead cedars on watershed nutrient export (D’Amore et al. 2009). Economically and culturally, yellow-cedar trees are important because they provide valuable products for Alaska Native communities and the forest industry (D’Amore et al. 2009). These coastal forests also provide forage for the Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), an important game animal throughout the region. Since the 1980s, much forest-related research in southeast Alaska has addressed the implications of various active forest management regimes on habitat of this commonly hunted species and biodiversity (McClellan 2005, Deal 2007); aspects of this research centered on old-growth habitat and the effects of land use practices, such as clearcutting or partial cutting on forage (Wallmo and Schoen 1980, Kirchhoff et al. 1983, Hanley 1993). To date, researchers have not addressed the effects of yellow-cedar decline on the availability of key forage species. Death of yellow-cedar and the shifts in plant community dynamics in forests affected by decline can have cascading effects on the human-natural system by affecting the ecosystem services these forests provide (Hennon et al. 2012).

We studied the process of forest development using a chronosequence to compare forests unaffected by widespread mortality with those affected at different time points over approximately one century. Considering size classes from seedlings to large trees across the chronosequence, our analysis of the conifer species populations at various life-history stages, including death, documented

Table 1. Published time-since-death estimates for dead standing (snag) yellow-cedar classes using various methodologies. Values are given as mean $\pm$ SD with range in parentheses where shown.

Snag classification	Stan et al. (2011) [†]	Hennon et al. (1990b) [‡]	Hennon et al. (1990b) [§]
Class I	4.7 yr $\pm$ 1.87	3.6 $\pm$ 3.2 (0–10)	...
Class II	12.56 $\pm$ 5.31	13.6 $\pm$ 6.9 (3–24)	8.5 $\pm$ 0.7 (8–9)
Class III	25.25 $\pm$ 9.87	26.2 $\pm$ 12.3 (12–52)	39.0 $\pm$ 15.7 (25–56)
Class IV	3 trees: 40, 58, 104	55.4 $\pm$ 25.2 (24–100)	51.2 $\pm$ 18.1 (27–96)
Class V	1 tree: 279	...	81.4 $\pm$ 22.0 (49–128)

Note: Ellipses indicate absent time-since-death estimates for specific snag classes in the corresponding study (Hennon et al. 1990b).

[†] Outer ring dates of increment cores taken from yellow-cedar trees in each snag class.

[‡] Trees with dead tops and most of the bole dead but a portion live to estimate time-since-death by counting rings in the formed live callus tissue to the dead bole.

[§] Release events in suppressed trees that neighbor dead yellow-cedar snags.

changes occurring in forests affected by decline, and extended a view of forest composition and structure into the future. We hypothesized that: (1) western hemlock and other conifers (non-yellow-cedar) increase in importance as the contribution of yellow-cedar to the conifer community structure is reduced over time, (2) seedling and sapling regeneration increases as yellow-cedars die and the canopy opens, (3) community composition of understory plants changes over time such that shrubs increase in abundance, and (4) the volume of key forage species for the Sitka black-tailed deer increases in forests affected by decline. Our study illustrates the long-term consequences for many plant species when a single tree species suffers from climate-induced mortality.

MATERIALS AND METHODS

Study area

Modern climate in the southeast region of Alaska is mild and hypermaritime with year-round precipitation, absence of prolonged dry periods, and comprised of comparatively mild season conditions (i.e., cooler summer and warmer winters) than continental climates at similar latitudes (Beier et al. 2008). Mean annual rainfall measured in Sitka and Gustavus, the two closest towns to the remote, outer coast study area, measure 2200 and 1700 mm, respectively. The high rainfall that occurs throughout the Alexander Archipelago, combined with its unique island geography, geologic history, and absence of fires maintain some of the most expansive old-growth forests found in North America. Five common conifer species occur on the northern range of the Archipelago: western

hemlock (*Tsuga heterophylla*, Raf., Sarg.), mountain hemlock (*Tsuga mertensiana*, Bong., Carrière), yellow-cedar, Sitka spruce (*Picea sitchensis*, Bong., Carrière), and shore pine (*Pinus contorta*, Douglas ex Loudon). These coastal forests are simple in composition yet often complex in age and tree structure (Deal 2007). Yellow-cedar occurs across a soil-drainage gradient from poorly drained bogs to well-drained soils on steeper slopes that often support more productive stands (Neiland 1971, Hennon et al. 2012).

This study occurs in the northern portion of the yellow-cedar population distribution and at the current latitudinal limits of forests affected by decline. We centered our investigation on protected lands in four inlets (Slocum Arm, Klag Bay, Dick's Arm, and Graves Harbor (N 57.44561, W 135.81128 to N 58.28759, W 136.73135) in the Alexander Archipelago on the outer coast of the West Chichagof-Yakobi Wilderness on Chichagof Island in the Tongass National Forest and Glacier Bay National Park and Preserve (GLBA). Aerial surveys were conducted in 2010 and 2011 to assess the presence of affected forests and to identify the edge of yellow-cedar dieback that occurs south of GLBA on Chichagof Island. Aside from a brief history of small-scale gold mining that occurred in several areas on Chichagof Island between 1906 and 1942, there is little evidence of human impact on these lands, making them ideal for studying ecological dynamics.

Plot selection

Drawing upon previous studies that estimated the time-since-death for five classes of standing dead yellow-cedar trees (Table 1) at various

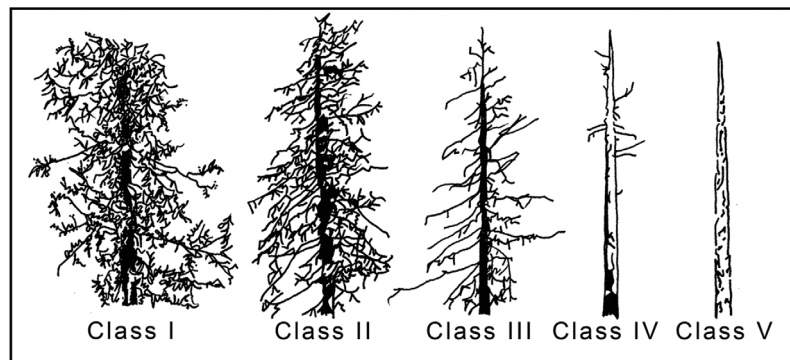


Fig. 1. Graphic representation of snag classes (adopted from Hennon et al. 1990b): Class I (dead foliage retained), Class II (twigs retained), Class III (secondary branches retained), Class IV (primary branches retained), and Class V (bole intact but no primary branches retained).

stages of deterioration (Fig. 1), our plot selection consisted of sequential steps, in the field, to sample forests representative from a range of time-since-death. Not all yellow-cedar trees in a forest affected by mortality die at once; mortality is progressive in forests experiencing dieback (Hennon et al. 1990a). Highly resistant to decay, these trees remain standing for up to a century after their death (Kelsey et al. 2005). As a result, they offer the opportunity to date disturbance, approximately, and to create a long-term chronosequence.

First, we stratified the study area coastline into visually distinguishable categories of “cedar decline status” (Table 2) by conducting boat surveys and assessing cedar decline status across 121.1 km of coastline in June 2011 and 2012. We traveled the coastline (92.9 km on Chichagof, 18.1 km in Graves Harbor, 10.1 km in Dick’s Arm) and made visual observations of live and dead yellow-cedar trees and their snag classes. We assigned cedar decline status to coastal forests at

100 m increments using a GPS Garmin 60 CSx (Garmin, Olathe, Kansas, USA). Next, using the ArcGIS 10.2 Geographic Information System software (ESRI 2011), we randomly generated plot locations in forests categorized during the coastline survey as follows: (1) live, unaffected by mortality; (2) recent mortality; (3) mid-range mortality; and (4) old mortality. Lastly, we controlled for basal area ($>35 \text{ m}^2/\text{ha}$) and key biophysical factors, including elevation ($<150 \text{ m}$) and aspect (NE facing plots, $0\text{--}90^\circ$) via methods described.

Plots were restricted to elevations less than 150 m, excluding northeast facing plots, to sample from low-elevation plots representative of conditions where yellow-cedar decline commonly occurs at this latitude (Hennon et al. 2012). Plots were randomly located between 0.1 and 0.5 km of the mean high tide to avoid sampling within the beach fringe area, and on slopes $<72\%$ to limit risk of mass movement (USDA Forest Service 2008). We excluded plots with a total

Table 2. Cedar decline status categories used for sampling stratification by visual observation of coastline across the study area. Plots were established according to methods described in four categories: live, recent mortality, mid-range mortality, and old mortality.

Cedar decline status	Snag classes/live trees observed
Live	Dominated by live yellow-cedar (YC) but trees may show signs of stress with Class I mortality present
Recent mortality	Dominated by Classes I and/or II, but Class III may be present
Mid-range mortality	Dominated by Class III, but Classes II and/or IV may be present
Old mortality	Dominated by Classes IV and V
Non-cedar	YC not present or present only as a minor component of the forest
Uncategorized	YC mortality present, but snag classes too varied to be typified by a single survey category

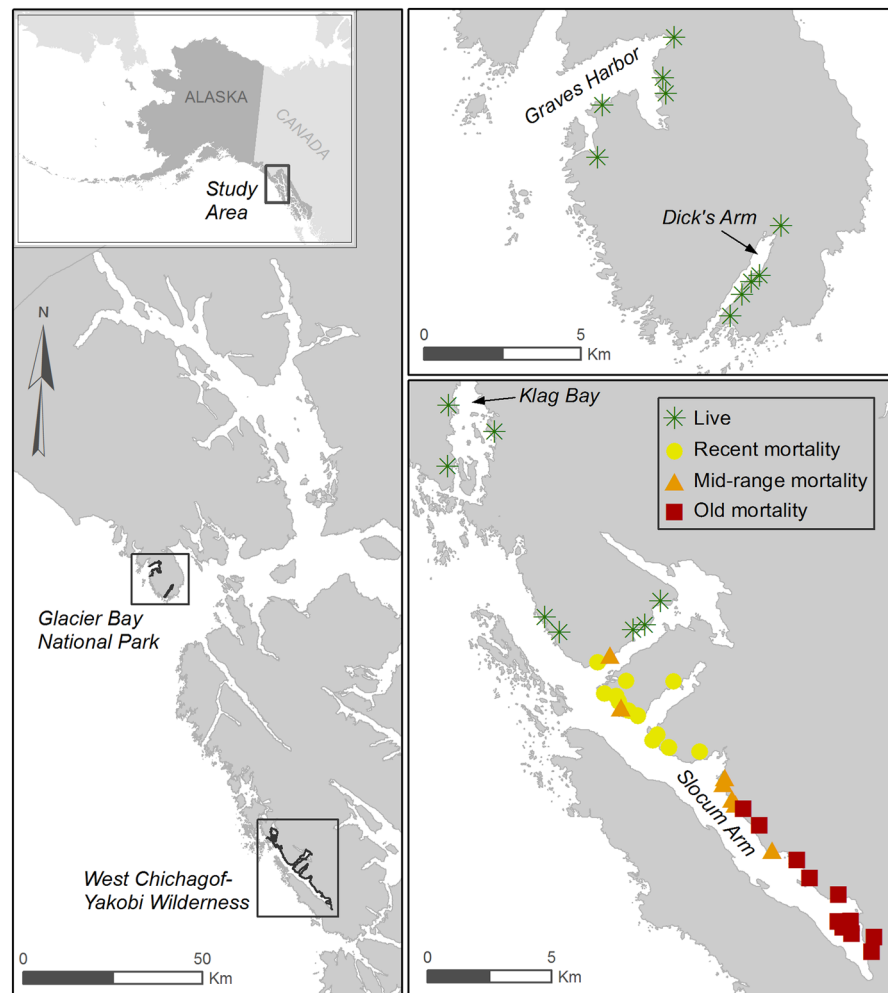


Fig. 2. Study area in southeast Alaska, locations of plots, and cedar decline status for each plot according to results from clustering analyses.

basal area $<35 \text{ m}^2/\text{ha}$ (live and dead) to avoid sampling below the optimal niche of yellow-cedar (Hennon et al. 2012). This control was performed in the field by point sampling to estimate basal area (Bell and Dilworth 1997) using a prism with a basal area factor (BAF) 2.5 (Van Laar and Akça 2007). Plots dominated by the presence of a creek bed or other biophysical disturbance (extreme windthrow) were eliminated from plot selection, due to the confounding influence of disturbance on the number of trees standing and species abundance. A minimum distance of 300 m was maintained between all plot centers. By restricting our sampling to these controls, our study was designed to examine the

process of forest development post-decline in low-elevation coastal forests with plot conditions typical for yellow-cedar mortality excluding bog wetlands, where yellow-cedar may co-occur sparsely with shore pine. After controlling for biophysical factors, 20 plots were sampled in live forests and 10 plots in each of the affected cedar status categories (recent mortality, mid-range mortality, and old mortality) for a total of 50 plots across the study area (Fig. 2).

Vegetation surveys

Data were collected in fixed, circular nested plots to capture a wide range of tree diameters and in quadrats within each plot to account for

spatial variability in understory vegetation. Forty plots were established and measured during the 2011 field season and 10 plots during the 2012 field season, through the seasonal window of mid-June to mid-August. Nested circular plots were used to sample trees and saplings as follows: (1) a 10.3 m fixed radius plot for trees ≥ 25.0 cm diameter at breast height (dbh), (2) a 6.0 m fixed radius plot for saplings < 2.5 cm dbh and ≥ 1 m height, and trees 2.5–24.9 cm dbh. We counted live saplings of each species to analyze the population dynamics for individuals that survive to this size class. For each tree, we recorded species, dbh to the nearest 0.1 cm, height to the nearest 0.01 m, dead or live, and for dead trees snag classes I–V. Eight quadrats at each plot (1×1 m, oriented 5 and 8 m from plot center along the four cardinal directions) were utilized to record understory plants and tree seedling densities. To provide an additional long-term view of species changes, we recorded counts for smaller conifer seedlings (< 10 cm height) (Deal et al. 1991), identifying western hemlock and mountain hemlock to genus, and other conifers to species. We noted presence/absence of each conifer species 10–99 cm, but did not sample this size class for individual counts. We recorded maximum height and percentage cover of each plant species observed according to the Daubenmire (1968) method on a continuous scale (1–100%). In unique cases where consistent identification to species was difficult (i.e., *Coptis asplenifolia* Salisb. and *C. trifolia* (L.) Salisb.; *Vaccinium ovalifolium* Sm., and *V. alaskaense* Howell), we combined observations but noted both species presence for total richness across the study area. Blueberries, *V. ovalifolium* and *V. alaskaense*, are similar in appearance and often synonymized (Vander Kloett 1988). Mosses and liverworts were recorded together as bryophytes within the quadrat. Sedges (*Carex* spp. and relatives of the Cyperaceae family) were recorded together but distinguished from true grasses (Poaceae).

We used hemispherical photography to assess canopy cover at each plot. Photographing from plot center at dbh camera height, we captured imagery in relatively uniform, overcast skies and consistently avoided any mid-day sun conditions (Fiala et al. 2006). To prevent diminished sharpness associated with consumer-grade cam-

eras (Frazer et al. 2001), we used a Sigma 4.5mm fish-eye lens (Aizu, Japan) on a professional-grade Canon 7D camera (Melville, New York, USA). Full-view images (180°) were processed using Gap Light Analyzer (Frazer et al. 1999) to yield percentages of canopy openness per plot as a proxy for light in understory analyses (Jarčuška 2008).

Data analysis

Clustering plots by cedar decline status.—To rigorously account for the timing of mortality relative to the coarse visual cedar decline status categorizations made by boat, we performed *k*-means clustering analyses (Ramette 2007) on the yellow-cedar population observed across the chronosequence by partitioning 50 plots into those affected by mortality and live “controls” for subsequent stages of analysis. Using observations of dead and live yellow-cedar trees at each of the 50 plots (total number of dead and live trees aggregated to the plot level for 804 trees), we stratified the plots into two groups for unaffected and affected forests. We then performed a *k*-means clustering analysis with the categorical snag classifications (Fig. 1) observed at the resulting 30 plots affected by mortality, assigning the a priori $k = 3$ for three affected status categories sampled: recent mortality, mid-range mortality, and old mortality. We restricted this analysis to yellow-cedar trees > 10 cm dbh (total number of individuals in snag classes I–V aggregated to the plot level for 478 trees) because the methods of dating time-since-death for yellow-cedar trees rely upon standing, larger trees (Hennon et al. 1990b, Stan et al. 2011). We analyzed the cluster stability by computing the Jaccard coefficient to measure similarity between resulting clusters, assessed by the bootstrap distribution of the Jaccard coefficient for each cluster compared with the most similar cluster in the bootstrapped datasets (Hennig 2007). Post hoc Fisher’s exact tests further clarified differences in the numbers of observed class I, II, and III snags between recent and mid-range mortality clusters (total number of individuals in each snag class aggregated to the plot level for 175 trees); observed class II, III, and IV snags between recent and mid-range mortality clusters (similarly aggregated, 167 trees), and between mid-range and old mortality clusters (similarly aggregated,

166 trees); and observed class III, IV, and V snags between mid-range and old mortality clusters (similarly aggregated, 200 trees). These analyses were performed in R (R Development Core Team 2012) using the GCLUS and FPC packages. This post-field methodology for plot stratification enabled us to refine the visual cedar decline status assigned in the boat surveys by clustering according to the observed populations of live yellow-cedar trees from the plot data.

Stand structure and regeneration.—We calculated the importance value (IV) for live conifers in the overstory as the sum of relative density, frequency, and basal area per species to characterize the stand structure and conifer composition (Curtis and McIntosh 1951) within each cedar decline status resulting from clustering analyses, and to make comparisons across the chronosequence of cedar decline status. For each species in three size classes (treelets, small trees measuring 2.5–9.9 cm dbh; small trees, 10–24.9 cm dbh; big trees, ≥ 25.0 cm dbh), we computed the following variables: density (D = number of individuals/ha), frequency (F = number of plots with the species present/total plots), and dominance ($Do = \Sigma$ basal area of individuals), and with the relative values (R) of these three parameters, the importance value was calculated as $IV = DR + FR + DoR$ (Guariguata et al. 1997, López and Dirzo 2007). Thus, the cumulative value for all tree species per size class in each cedar decline status was 300%.

In assessing regeneration, we focused analysis on seedling counts (< 10 cm height) and saplings (≤ 2.5 cm dbh and ≥ 1.0 m height) to consider established plants. We used Kruskal–Wallis tests and performed permutation tests on the measure of central tendency (1000 permutations) to examine differences in mean seedling and sapling abundance (all species) across the four cedar decline status categories. Using presence/absence sapling data, we calculated the probabilities of finding each individual conifer species in the sapling life stage in each cedar decline status and generated binomial confidence intervals to estimate uncertainty using the Wilson score interval. We used a two-part modeling approach to determine the probability of species' occurrence in cedar decline status and to test for significant effects of cedar decline status on each species' abundance in the sapling stage. This method was selected to account for overdispersion in zeros in

the individual abundance data for the conifer species in the sapling life stage (zero counts were: yellow-cedar, 32; western hemlock, 10; mountain hemlock, 23; Sitka spruce, 15; shore pine, 42). In the first step, the data were considered as zeros versus non-zeros and a binomial model was used to model the probability of observing a zero-value; in the second step, non-zero observations were modeled with a zero-altered Poisson (ZAP) model (Cunningham and Lindenmayer 2005, Zuur et al. 2009). Canopy openness and cedar decline status (as a factor) were included in the models as explanatory variables to predict species presence/absence and sapling abundance. Best models were selected based upon AIC values. These analyses were performed in R using the PSCL, MHURDLE, and BINOM packages. We determined the IV for saplings in each cedar decline status on the basis of relative density and relative frequency (but omitting basal area), such that the IV of all species would sum 200%. To compare the persistence of saplings to treelets in the early stages of stand development, we calculated the ratio of saplings to live treelets per hectare at each plot and tested for significant differences between live $\sim$ recent mortality and live $\sim$ mid-range mortality using Wilcoxon rank sum tests. Probabilities calculated for species occurrence in the size class 10–99 cm in each cedar status were used for comparison with seedling and sapling results to assess trends in survival.

Understory diversity, community composition, and key forage species.—We analyzed the understory data collected at plots measured during the 2011 field season on Chichagof Island to avoid any confounding effects of seasonal variation in understory plant growth (cover, height). Plots on Chichagof Island ($n = 38$, after removing two plots from the dataset; see *Results: Cedar decline status*) were measured between early July and mid-August during peak summertime growth, whereas data collected in GLBA ($n = 10$) were restricted to early June due to the timing of permissible weather conditions for accessing the outer coast. The Shannon diversity index [$H = -\Sigma p_i \ln(p_i)$, where p_i is the proportion of the total percent cover measured represented by species (taxa, or grouping) i at eight quadrats per plot] was used to assess differences in plant diversity (richness and evenness of vascular plants and

plant growth forms, i.e., functional groups; Chapin 1993, Díaz and Cabido 2001) post-decline. We tested for significant differences across and between cedar decline status with ANOVA and Tukey HSD tests. Data were tested for normality using the Shapiro–Wilk W test and homogeneity of variance using Bartlett's (1937) test.

We calculated the abundance of understory plant groupings (forbs, shrubs, ferns and lycophytes, graminoids, bryophytes; mosses and liverworts) for each plot by averaging canopy cover measurements for the eight quadrats. Groupings (Appendix A) were delineated first by growth habitat (shrubs and forbs) in the PLANTS Database (USDA, NRCS 2014) and then further distinguished to ferns, lycophytes, and graminoids according to Pojar and MacKinnon (1994). We then used permutational multiple analysis of variance (PERMANOVA, $\alpha = 0.05$) based upon Bray–Curtis dissimilarities of the untransformed multivariate data (five groups) to assess whether the cedar decline status hosted significantly different communities. We visualized these differences with nonmetric multidimensional scaling (nMDS; Anderson 2001, Ramette 2007).

We investigated changes in volume of key forage species for Sitka black-tailed deer to examine potential indirect effects of climate change on forage. We selected five species considered common forage species for deer in the region: deer fern (*Blechnum spicant* (L.) Sm.), bunchberry (*Cornus canadensis* L.), strawberryleaf raspberry (*Rubus pedatus* Sm.), threeleaf foamflower (*Tiarella trifoliata* L.), Alaska/oval-leaved blueberry (*Vaccinium alaskaense/ovalifolium*) (Hanley and McKendrick 1985, Kirchhoff and Hanley 1992, Deal 2001), and compared volume across the chronosequence. Volume (as a proxy for growth, or expansion or contraction of each species) was calculated by multiplying the percentage cover by height and averaging the product across quadrats for each species per square meter at each plot (Anderegg et al. 2012).

We tested for significant differences in abundance for the shrub, bryophytes, and graminoid groupings and volume for the three species between the live and affected status (live ~ recent mortality, live ~ mid-range mortality, live ~ old mortality) using permutation tests, Krus-

kal–Wallis, and Wilcoxon rank sum tests with Bonferroni corrections—a particularly conservative choice for multiple comparisons with non-normally distributed data. Differences for all statistical tests performed were significant if $p \leq 0.05$.

RESULTS

Cedar decline status

Standing dead trees constituted 3.0–81.0% of the total basal area at plots across the study area, with the largest percentage of dead occurring in forests classified as mid-range mortality. On average, dead yellow-cedar comprised 13.4%, 71.9%, 84.5%, and 82.6% of the total yellow-cedar basal area in the live, recent mortality, mid-range mortality, and old mortality cedar status, respectively (Table 3).

Clustering results were used to assign cedar decline status to each plot for subsequent comparisons in overstory and understory vegetation between live forests and those affected by mortality (Fig. 3). Only two of the 20 plots established in the live cedar status area clustered with those affected by decline; all other plots clustered according to field stratification of live or affected status. We removed these two plots from the dataset, because clustering results and field observations affirmed that these plots experienced relatively higher levels of background tree death compared with other live plots but not continued mortality representative of forests affected by widespread decline. Cluster stability analysis resulted in no dissolved clusters (Hennig 2008) and proved highly stable with Jaccard coefficients of 0.94 and 0.96. Five of the 30 plots established in the affected forest types were reclassified; all other plots in the affected forests clustered according to the field classification. Cluster stability analysis of the affected plots resulted in three dissolved clusters and proved moderately to highly stable with Jaccard coefficients of 0.64, 0.72, and 0.90. Statistical comparisons confirmed significant differences in the distributions of snag classes between clusters. Eighteen plots clustered in the live status: 12 in recent mortality, 7 in mid-range mortality, and 11 in old mortality. Clustering results did not differ when performing k -means clustering analysis with $k = 4$ on live trees and snag classes observed. However, we present

Table 3. Mean basal area (trees ≥ 2.5 cm dbh) of live and standing dead trees and saplings within each cedar decline status and mean density of live and standing dead trees and saplings within each cedar decline status.

Species	Basal area (m ² /ha)				Density (stems/ha)					
					Treelets		Small trees		Big trees	
	Live	Dead	Total	% Dead	Live	Dead	Live	Dead	Live	Dead
Live										
Yellow-cedar	34.6	5.4	40.0	13.4	510	210	695	165	177	15
Hemlock										
Western	17.5				230		255		113	
Mountain	4.7				80		65		33	
Western + mountain		3.1	25.4	12.4		110		100		13
Sitka spruce	3.0	0.9	4.0	23.2	60	10	50	15	15	7
Shore pine	1.6	0.5	2.1	23.8	5	0	25	5	13	3
All species	61.4	10.0	71.4	14.0	885	335	1,090	290	352	40
Recent mortality										
Yellow-cedar	15.2	38.8	54.0	71.9	270	135	188	413	100	270
Hemlock										
Western	8.1				285		233		28	
Mountain	1.7				68		60		8	
Western + mountain		2.2	12.0	18.4		120		53		13
Sitka spruce	4.2	1.3	5.6	24.0	120	45	83	8	20	13
Shore pine	0.2	0.0	0.2	0.0	0	0	0	0	3	0
All species	29.4	43.6	73.0	59.7	743	315	563	495	158	300
Mid-range mortality										
Yellow-cedar	5.7	30.9	36.6	84.5	373	360	116	463	26	180
Hemlock										
Western	7.9				463		283		13	
Mountain	1.9				129		64		9	
Western + mountain		5.8	15.6	37.1		180		180		4
Sitka spruce	2.0	0.0	2.0	0.0	64	0	13	0	9	0
Shore pine	2.3	1.5	3.7	39.5	26	0	13	26	17	9
All species	19.8	39.8	59.6	66.8	1,054	566	489	694	73	197
Old mortality										
Yellow-cedar	7.8	36.9	44.7	82.6	237	286	131	507	41	237
Hemlock										
Western	17.2				581		344		82	
Mountain	4.8				213		73		22	
Western + mountain		8.1	30.1	27.0		213		139		25
Sitka spruce	0.9	0.7	1.6	43.1	196	16	16	25	6	0
Shore pine	0.7	0.2	0.9	17.6	0	0	16	0	3	3
All species	31.4	46.9	78.3	59.9	1,227	605	581	704	153	265

Notes: Density is reported in three size classes: treelets (2.5–9.9 cm dbh), small trees (10–24.9 cm dbh), and big trees (≥ 25.0 cm dbh). Dead western hemlock and mountain hemlock are reported together, given uncertainty in identifying the decayed trees in this genus to the species level. “All species” include dead unknown individuals that were confirmed not to be yellow-cedar but were otherwise undistinguishable.

results from the two stages of clustering to show cluster stability at the two stages (between the live and affected plots, and between the plots affected by decline with temporal variation). All subsequent analyses across the chronosequence used the stratification of live forests according to the first clustering results and affected forests according to the second clustering results to distinguish cedar decline status.

Conifer community

Stand structure and composition.—All five species of conifers were present in the study area in sapling and tree form. We measured 2064 trees

and 882 saplings across the 48 plots that resulted from clustering analyses. Tree diameters for all species present ranged from 2.5 to 108.1 cm, in a reverse-J size-frequency distribution often associated with multiage stands (Assmann 1970, O'Hara 1998, 2014). Heights ranged from 1.5 to 32.0 m.

Total basal area of all live and dead standing trees (≥ 2.5 cm dbh) in the plots ranged from 36.01 m²/ha to 145.55 m²/ha (71.74 ± 19.72 m²/ha, mean $\pm$ SD). One-way ANOVA did not show a significant difference in total basal area across the four status categories ($F_{1,46} = 0.143$, $p = 0.707$; Table 3). Average density of all standing trees

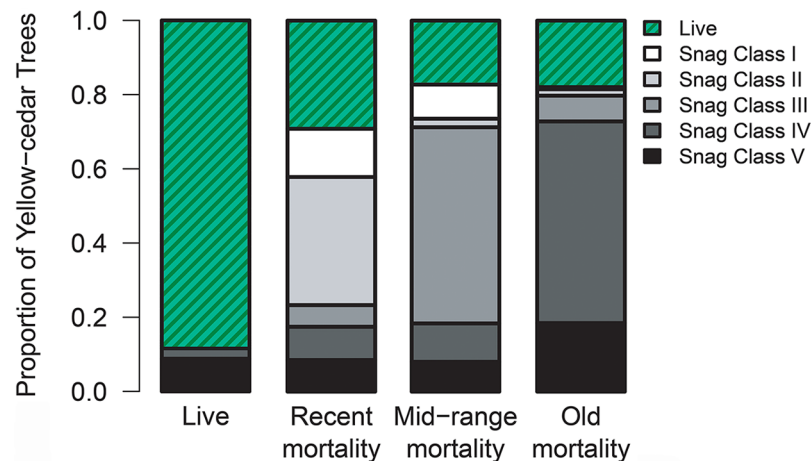


Fig. 3. Proportion of live yellow-cedar trees and snags (by snag class) for trees ≥ 10 cm dbh observed in each cedar decline status. Plots were stratified by cedar decline status according results from *k*-means clustering analyses; $N = 48$, $n = 18$ in live forests, $n = 12$ in recent mortality, $n = 7$ in mid-range mortality, and $n = 11$ in old mortality.

(live and dead, ≥ 2.5 dbh) was as follows: 2992 trees/ha in the live cedar status, 2574 trees/ha in recent mortality, 3073 trees/ha in mid-range mortality, and 3535 trees/ha in old mortality (Table 3). Live big trees (≥ 25 dbh) constituted 11.8%, 0.06%, 0.02%, and 0.05% of the stand density in each cedar decline status. We did not find significant differences between status categories in the absolute density of the total dead and live trees in each size class; however, averages (Table 3) indicate increasing trends of stand density. We observed a significant increasing trend in average canopy openness between live forests ($29.3 \pm 6.0\%$) and those recently affected by decline ($35.2 \pm 6.4\%$), and in mid-range mortality (38.4 ± 5.9 ; $W = 17$, $p = 0.012$). However, there was no significant difference in canopy openness between live and old mortality, indicating that post-decline stand development reaches greater canopy closure across the chronosequence.

The community composition of the five conifer species in the live status was consistent across the three size classes of trees and similar to structure described by Martin et al. (1995) for the western hemlock–yellow-cedar plant community. This composition shifted significantly across the chronosequence (Fig. 4). The importance of yellow-cedar in the conifer community structure was greatly reduced in forests affected by decline.

Between live and old mortality, yellow-cedar dropped in importance from 135%, 162%, and 150% (big trees, small trees, and treelets) to 84%, 73%, and 64%, respectively. These reductions occurred in a staggered process across size classes. Relative frequencies, density, and dominance of big yellow-cedar trees remained high in recent mortality, despite the death of some big trees (Table 3), and live trees commonly showing symptomatic signs of stress, such as crown reduction. Western hemlock was the most important species in old mortality across all size classes (128%, 153%, and 141% for treelets, small trees, and big trees, respectively), as well as saplings (92%). Mountain hemlock maintained its species rank-order as third most important species across all size classes in old mortality. Shore pine and Sitka spruce remained minor components of the post-decline forest, particularly as small and big trees in old mortality. The increased importance of shore pine as big trees in mid-range mortality was likely indicative of pre-existing community composition.

The community structure of the sapling community in forests affected by the dieback was distinguished by the diminished importance of yellow-cedar (57% to 4%, from live forests to old mortality) and increased importance in other conifer species, except shore pine. In species rank-order, the sapling community retained its

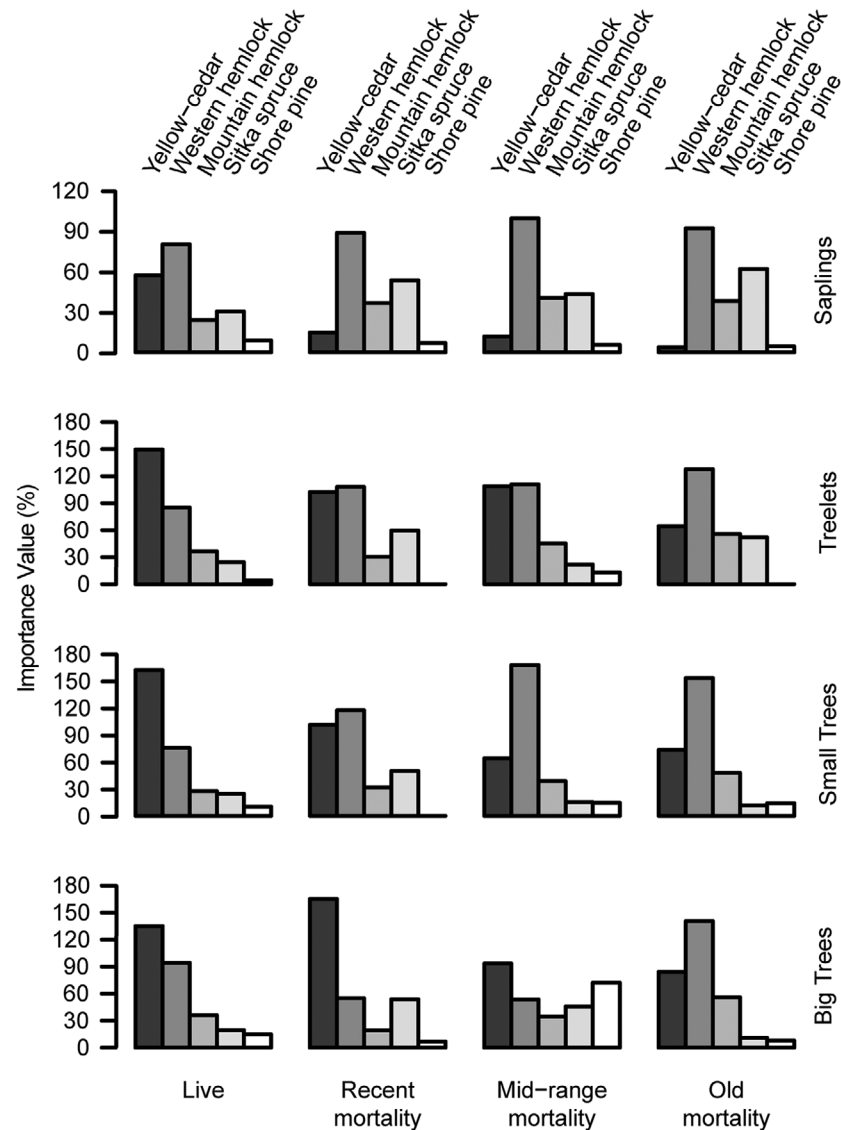


Fig. 4. Importance value (IV) of conifer species in each cedar decline status calculated for live trees and saplings in four size classes: saplings (<2.5 cm dbh and ≥ 1.0 m height), treelets (2.59.9 cm dbh), small trees (1024.9 cm dbh), and big trees (≥ 25.0 cm dbh). Each value reported as a percentage is a sum of relative density, relative frequency, and relative dominance.

structure across affected forests (recent mortality, mid-range mortality, old mortality), as western hemlock, mountain hemlock, and Sitka spruce competed to regenerate.

Regeneration.—Consistent with our hypotheses, seedling (<10 cm) abundance increased post-decline (Appendix B). We observed trends of increased abundance across the chronosequence, with maximum density occurring in old mortality. There was a marginally non-significant

difference in seedling abundance across categories and a significant difference in seedling abundance with a permutation test ($p = 0.015$). Wilcoxon rank sum tests between the live and affected status categories showed a significant increase in seedling abundance between live and old mortality ($W = 46$, $p = 0.049$). Yellow-cedar seedlings occurred at 47 of 48 plots, and yellow-cedar seedling abundance significantly decreased between live and recent mortality ($W = 192$, $p <$

0.001); mid-range mortality ($W = 120.5$, $p < 0.001$); and old mortality ($W = 171.5$, $p < 0.001$). Yellow-cedar seedling abundance was reduced by 69.4%, 80.0%, and 65.7% from the live forests to recent, mid-range, and old mortality, respectively. Hemlock seedlings were found at all plots throughout the study area and significantly increased in abundance in old mortality ($W = 38.5$, $p = 0.016$). Mean hemlock seedling abundance increased 48.7%, 51.2%, and 260.1% from the live forests to recent, mid-range, and old mortality, respectively. We found no significant differences in Sitka spruce nor shore pine seedling abundance across the four cedar decline status categories ($H = 5.4316$, $df = 3$, 0.14 ; $H = 2.9369$, $df = 3$, $p = 0.401$).

Sapling abundance increased post-decline with maximum density occurring in mid-range mortality. There was a marginally non-significant difference in sapling abundance ($H = 7.153$, $df = 3$, $p = 0.067$) across categories. Wilcoxon rank sum tests between the live and affected status categories showed a marginally non-significant difference in sapling abundance in mid-range mortality ($W = 26$, $p = 0.070$). Relatively, sapling densities were more likely to occur in mid-range mortality.

Our two-step models for sapling occurrence and abundance helped explain the varying conditions under which each species tended to persist as individuals in the sapling stage. The inclusion of canopy openness improved two-step models for sapling occurrence and abundance for all five species (Fig. 5), and specific cedar status categories were significant predictors for species sapling abundances (see Appendix C for outputs of selected models). Canopy openness was a significant positive predictor of sapling occurrence for mountain hemlock ($p = 0.015$) and shore pine ($p = 0.021$), as saplings for these species were found on more open plots. For western hemlock, neither cedar decline status nor canopy openness was a significant predictor of occurrence, as western hemlock regeneration was common across the study area. Openness was a significant predictor of yellow-cedar ($p < 0.001$), western hemlock ($p = 0.063$, marginally significant), and spruce sapling ($p < 0.001$) abundance (Fig. 5B) such that greater sapling density occurred on plots more open for western hemlock and yellow-cedar, and less open for

spruce. Affected status categories were each significant positive predictors of western hemlock abundance with maximum abundance occurring in mid-range mortality [$\beta(\text{SE}) = 0.305(0.138)$, $p = 0.027$; $\beta(\text{SE}) = 0.674(0.148)$, $p < 0.001$; $\beta(\text{SE}) = 0.651(0.143)$, $p < 0.001$]. Recent mortality was a significant, positive predictor of mountain hemlock abundance in the two-step model ($p = 0.039$), suggesting that mountain hemlock may best compete with western hemlock in the early stages of post-decline stand development. The probabilities of each species occurrence in the 10–99 cm size class followed similar trends in magnitude and direction to saplings (Fig. 5A). Our model findings clarified the site conditions favorable to different species, as shaped by both canopy openness and yellow-cedar mortality.

The probability of occurrence for yellow-cedar saplings (Fig. 5A) was significantly reduced between live forests and old mortality (0.56–0.09; $p = 0.027$), with a steadily decreasing trend across the chronosequence. In the 10–99 cm size class, the probability of yellow-cedar occurrence was reduced from 0.61 (live) to 0.25, 0.14, and 0.18 (recent, mid-range, old, respectively). Live and recent mortality were significant predictors of yellow-cedar sapling abundance with greater abundance in the live status and on more open plots.

Saplings and treelets were typically dense in the mid-range mortality status. We found a significant increase in the ratio of saplings to live treelets between live and recent mortality ($W = 60$, $p = 0.044$) and a marginally significant increase between live status and mid-range mortality ($W = 36$, $p = 0.109$). Competition increased in the lower canopy, as regeneration occurred post-decline and individuals survived into the treelet size class (Table 3).

Understory plant community

Species richness and diversity.—Fifty-one taxa of vascular plants (excluding conifers) were identified (Appendix A): 37 were present in live status, 37 in recent mortality, 39 in mid-range mortality, and 43 in old mortality. We found no significant differences in H' of vascular plants across the chronosequence ($F_{1,36} = 1.152$, $p = 0.36$; Fig. 6A), but for H' of functional groups, we found significant differences in diversity ($F_{3,34} = 7.212$,

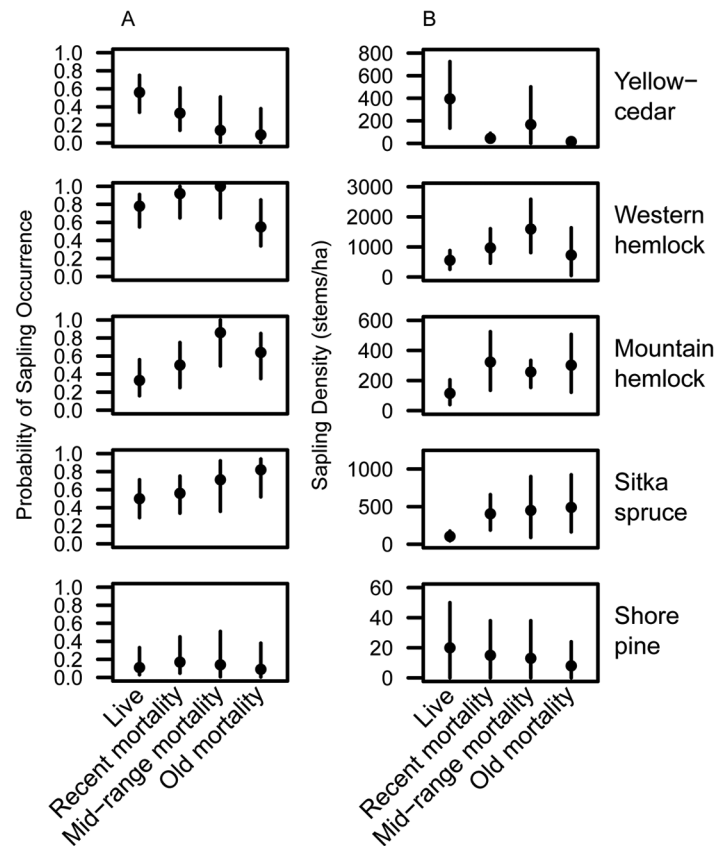


Fig. 5. Probability of sapling occurrence (A) and sapling density (B) for five conifer species in each cedar decline status. Error bars indicate the 95% confidence intervals, generated by bootstrapping the data (sampling means with replacement 1000 times) and selecting the 2.5th and 97.5th percentiles of the density distribution and using the Wilson score interval for robustness to small sample sizes for probabilities. Statistical tests were performed using the absolute data and a two-step model.

$p < 0.0001$; Fig. 6B). Results of the Tukey's HSD on the 95% family-wise confidence interval showed highly significant differences in the functional plant diversity between live and recent mortality ($p = 0.003$); live and mid-range mortality ($p = 0.008$), and significant, but to a lesser extent, differences between live and old mortality ($p = 0.021$).

Community composition by functional groups.—The community composition of understory plants differed significantly across the chronosequence (PERMANOVA: $F = 5.5548$, $p = 0.001$) and were driven primarily by differences in bryophyte, graminoid, and shrub abundance (Fig. 7A). We found highly significant differences in abundance of shrubs ($H = 15.1901$, $df = 3$, $p = 0.002$), graminoids ($H = 14.7464$, $df = 3$, $p = 0.002$),

and significant, but to a lesser extent, differences across cedar decline status categories in bryophytes ($H = 10.994$, $df = 3$, $p = 0.0178$), ferns and lycophytes ($H = 10.9725$, $df = 3$, $p = 0.012$), and forbs ($H = 9.2686$, $df = 3$, $p = 0.026$; Fig. 7B). Graminoid abundance increased significantly in recent mortality ($W = 11$, $p = 0.021$), but no significant differences in graminoid abundance were observed between live status and mid-range mortality or old mortality ($W = 9$, $p = 0.15909$; $W = 46$, $p = 1.000$). Shrubs increased in mid-range mortality and old mortality compared with live ($W = 2$, $p = 0.625$; $W = 13.5$, $p = 0.029$), but not significantly in recent mortality. Bryophytes decreased significantly in recent mortality ($W = 85.5$, $p = 0.007$); a decrease was marginally significant in mid-range and old mortality ($W =$

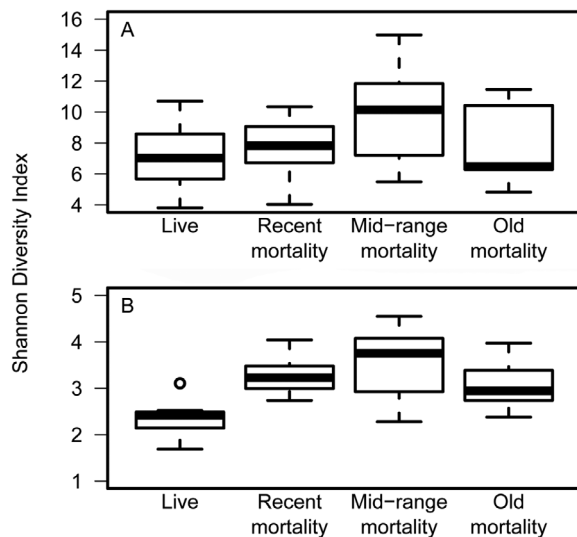


Fig. 6. Shannon diversity index (H') for vascular plants identified to the species level (A) and functional groups (B) whiskers, minimum and maximum values with outliers [circles], i.e., twice the interquartile range subtracted and added from the first and third quartile [bounds of boxes]; solid line, medians).

41, $p = 0.088$; $W = 70$, $p = 0.093$). Due to small sample size with bryophyte data missing at one plot in mid-range mortality, the results between live and recent mortality were marginally significant with the Wilcoxon rank sum test but highly significant with a permutation tests ($p = 0.003$; Fig. 7B). The patterns of changes observed indicate herbaceous plants responded relatively rapidly to the forest dieback in recent and mid-range mortality, whereas significant increases of shrub abundance occurred in latter stages of forest development post yellow-cedar decline.

Forage species.—The average volume of all five key forage species examined increased in forests affected by decline (Fig. 8). Results of the Kruskal–Wallis tests for average volume (m^3/m^2) calculated for each species revealed significant differences for each species tested (blueberry: $H = 18.41$, $\text{df} = 3$, $p < 0.001$; bunchberry dogwood: $H = 9.0851$, $\text{df} = 3$, $p = 0.028$; deer fern: $H = 10.01$, $\text{df} = 3$, $p = 0.018$; strawberryleaf raspberry: $H = 12.52$, $\text{df} = 3$, $p < 0.01$; threeleaf foamflower: $H = 10.1$, $\text{df} = 3$, $p = 0.018$). All statistically significant differences across and between status categories were robust to volume calculations using average height as opposed to

maximum height. Average volume of Alaska blueberry/oval-leaf blueberry increased 900% from live to old mortality. Deer fern average volume increased 200% from live to recent mortality and 500% from live to mid-range mortality. Bunchberry dogwood increased 100% from live to mid-range mortality. Trends observed in changes of the shrub, forb, and fern species volume were consistent with shifts in community composition of their respective functional plant groupings.

DISCUSSION

The changes observed across the chronosequence provide strong evidence that this species dieback associated with climate change can result in a temporally dynamic forest community distinguished by the diminished importance of yellow-cedar, an increase in graminoid abundance in the early stages of stand development, and a significant increase in shrub abundance and volume over time. Tree mortality timing and intensity, as characterized by our stratified sampling of cedar decline status, played an important role in determining the understory community composition and overstory processes of stand re-initiation and development. Our results highlight the ways in which widespread mortality of one species can create opportunities for other species and underscores the importance of considering long-term temporal variation when evaluating the effects of a species dieback associated with climate change. Methods for predicting future changes in species distributions, such as the climate envelope approach, rely upon statistical correlations between existing species distributions and environmental variables to define a species' tolerance; however, a number of critiques point to many factors other than climate that play an important role in predicting the dynamics of species' distributions (Pearson and Dawson 2003, Elith and Leathwick 2009). Given the different ecological traits among species, climate change will probably not cause entire plant communities to shift en masse to favorable habitat (Hampe 2004, Heikkinen et al. 2006, Hennon et al. 2012). Although rapid climatic change or extreme climatic events can alter community composition (Walther et al. 2002), a more likely scenario is that new

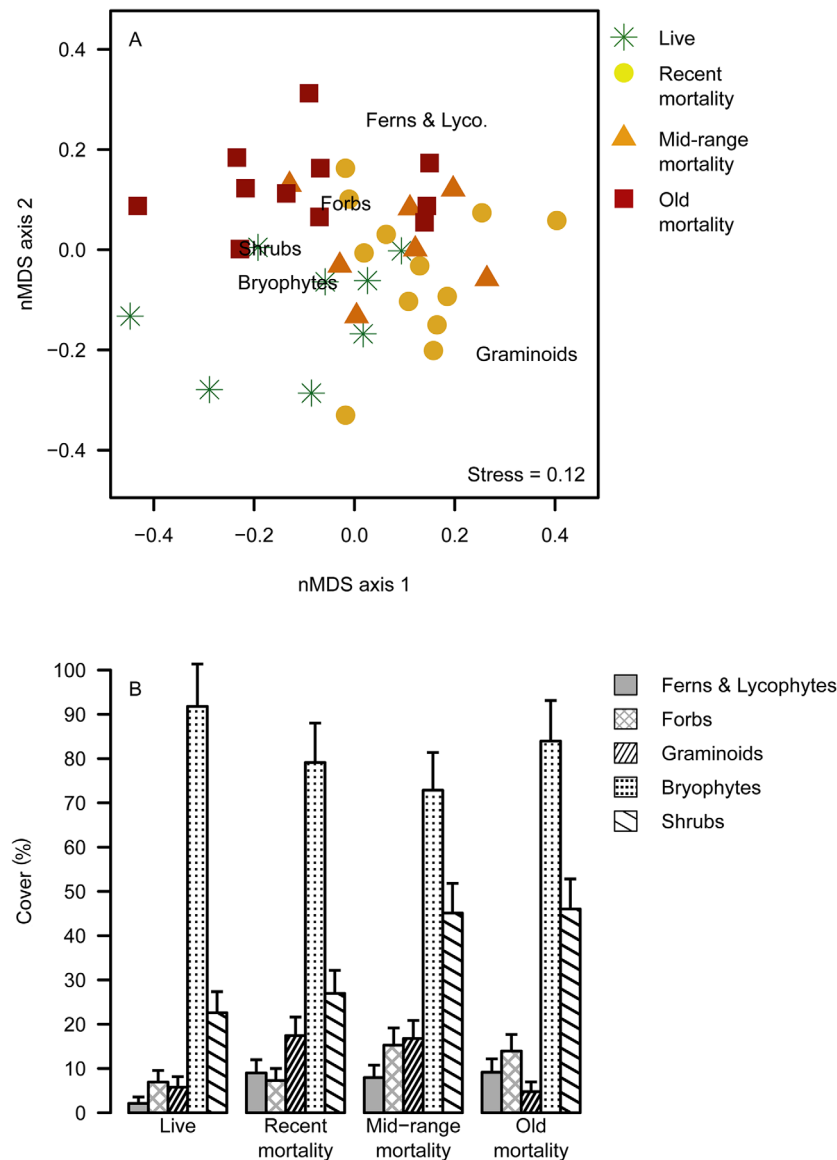


Fig. 7. Nonmetric multidimensional scaling (nMDS) plot of functional plant group composition in live forests and those affected by decline (distance between points corresponds to the dissimilarity in community composition) (A) and percent cover of functional plant groupings in the understory within each cedar decline status (B). Cover at each individual plot was calculated as an average of observations from eight quadrats. Error bars indicate a 95% confidence interval generated by bootstrapping the data (sampling means with replacement 1000 times) and selecting the 2.5th and 97.5th percentiles of the distribution.

assemblages will appear (Webb and Bartlein 1992). As vulnerable species drop out of existing ecosystems, resident species will become more competitive and new species may arrive through migrations (Hennon et al. 2012).

Individual species traits may also help explain

the process of forest development in forests affected by widespread mortality, as the most abundant species may be those with traits that make them well-adapted to changing biotic and abiotic conditions (Van der Putten et al. 2010).

We were unable to evaluate the independent

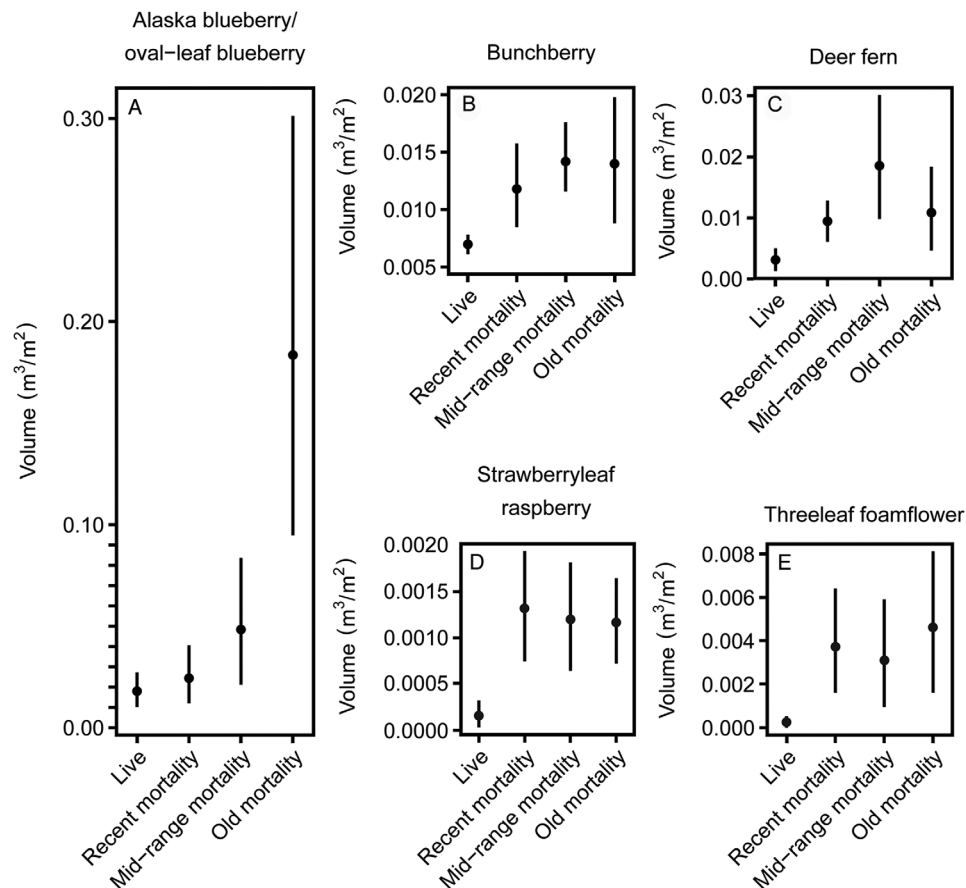


Fig. 8. Mean volume $\pm$ SD (95% confidence interval) for selected forage species in each cedar decline status (number of plots with eight quadrats per plot). Standard deviation was calculated as the bootstrapped standard error of the mean; the 95% confidence interval was generated by selecting the 2.5th and 97.5th percentiles of the bootstrapped distribution (sampling means with replacement 1000 times). Statistical tests were performed using the absolute data.

effect of soil saturation on canopy openness, but the fact that canopy openness was a significant predictor of shore pine and mountain hemlock sapling occurrence suggests the important roles of soil conditions (e.g., drainage) and light in determining which species are more likely to regenerate. Both species are known to have preferences for wet soils and scrubby open forests (Burns and Honkala 1990, Pojar et al. 1991, Pojar and MacKinnon 1994, Martin et al. 1995), and canopy openness in forests affected by decline has two driving components: soil saturation and crown deterioration caused by yellow-cedar death (D'Amore et al. 2009, Hennon et al. 2010). Young mountain hemlock seedlings, for example, grow best in partial shade (Dahms and

Franklin 1965), likely explaining why this species regenerated relatively well as saplings in recent mortality before canopy openness increased further. In contrast, western hemlock is known to tolerate a wide range of soil and light conditions for establishment and growth (Klinka et al. 2000) and seeds prolifically, as does Sitka spruce (Minore 1979, Klinka et al. 2000). Species can also respond to varying light conditions with differential growth responses. Western hemlock reached maximum growth rate when exposed experimentally to relatively high light intensities, whereas bunchberry responded most strongly to relatively low light intensities (Hanley et al. 2014). Although Sitka spruce was the second most important species in sapling regeneration in

the affected forests, this species played a less important role in the conifer community composition in subsequent stages of stand development. Spruce has been found to have lower regeneration than western hemlock on disturbed sites but higher survival rates; however, western hemlock regeneration that existed prior to disturbance formed a significant and dominant position in the future stand (Deal et al. 1991). In old mortality, the relatively high density of small, dead trees, low density of big, live trees, and high percentage of dead basal area (Table 3) suggest that although the Sitka spruce regenerates on plots less open, the species may be outcompeted by western hemlock over time. At the fine-scale, species traits can play important and even predictable roles in determining the establishment and growth of individuals under changing site conditions. These fine-scale interactions collectively shape community responses to the species dieback.

Conifer community

Our study documented significant losses in the yellow-cedar population but not extirpation. These directional changes likely extend beyond the temporal period of our chronosequence due to the diminished regeneration. The temporal dynamics of decreased yellow-cedar importance in each tree size class across the chronosequence suggest that yellow-cedar decline may be more likely to affect smaller trees first, whereas larger tree mortality occurs in a staggered process. Previous research has shown that surviving yellow-cedar trees in declining stands can produce larger growth rings but with greater interannual variability after the onset of decline (Beier et al. 2008), and that climate thresholds for the survival and reproduction of individuals can vary across life-history stages (Jackson et al. 2009). Reductions in yellow-cedar sapling occurrence and abundance in forests affected by decline indicate significant, long-term reductions in species abundance across larger size classes. Whether these reductions are caused by seed limitation, changes in seedling germination conditions, herbivory, or other mortality mechanisms is beyond the scope of our study. Although we did not count individuals in the 10–99 cm size class or dead saplings, our seedling and sapling findings indicate reduc-

tions in yellow-cedar over time and consistent rank-order of other conifer species (western hemlock, Sitka spruce, mountain hemlock) competing in sapling stage in the affected forests. Ramage et al. (2011) similarly found tanoak unlikely to regenerate successfully in forests affected by sudden oak death, a disease disturbance. Yellow-cedar appear maladapted to forests affected by decline for the foreseeable future.

We observed a process of stand development similar to forests affected by host-specific insect or disease disturbance, distinguished by an increase in regeneration while surviving trees release and saplings advance into the overstory. The results of our comparisons of total sapling density across the chronosequence indicate a re-initiation phase (*sensu*; Oliver and Larson 1996) that occurs post-decline. We found no significant difference between canopy openness in live forests compared with old mortality, significant increases in canopy openness in recent and mid-range mortality, and an overall steady increase in stand density across the chronosequence. These results document stand advancement toward canopy closure over time, indicating development of a relatively mature forest distinguished by changes in conifer community composition. We were unable to date the precise onset of widespread mortality at each plot; our estimates of temporal dynamics of stand re-initiation and advancement (Fig. 9) are informed by time-since-death estimates for snags observed at each plot. Snag class estimates suggest that widespread mortality began 81.4 ± 22.0 years ago for the old mortality cedar decline status and indicate approximately 50–100 years for stand advancement toward canopy closure.

Consistent with our hypotheses, we found an increase in the importance of western hemlock across all size classes as the importance of yellow-cedar was greatly reduced over time in the affected forests. It has been previously hypothesized that declining yellow-cedar forests on the northern extent of the yellow-cedar population distribution may convert to scrub forest or open bog, as western hemlock is not able to exploit some soil conditions favorable to yellow-cedars (D'Amore et al. 2009). In contrast but consistent with prolific hemlock regeneration found in old-growth hemlock-spruce forests

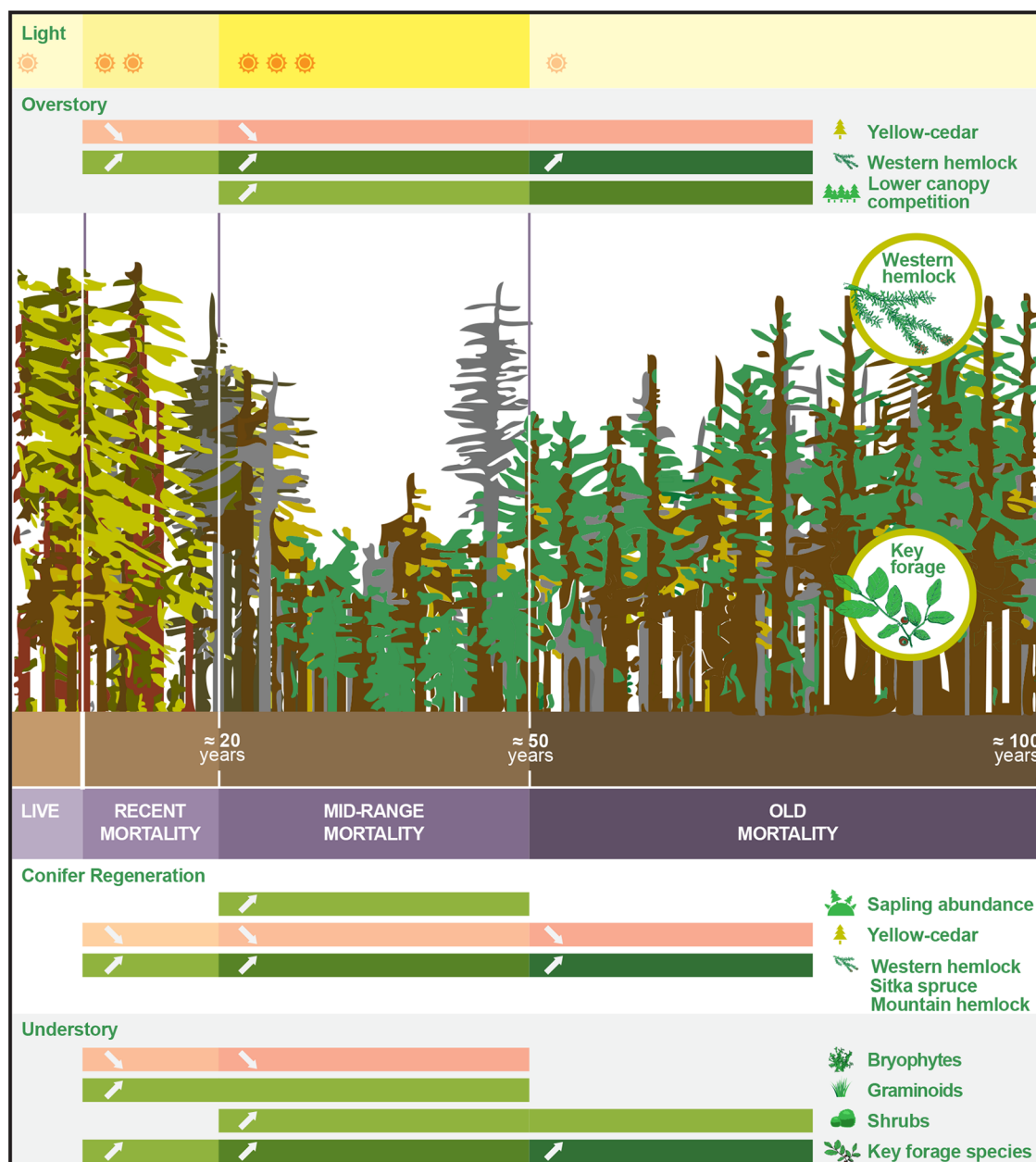


Fig. 9. Conceptual diagram depicting observed patterns of forest development following onset of yellow-cedar decline. Year ranges presented are estimates, because mortality is progressive, and estimates of time-since-death (mean $\pm$ SD) for snag classes overlap. Dead yellow-cedar trees in individual snag classes were also present across the chronosequence. Arrows illustrate direction of change (increase or decrease) and shading indicates relative intensity of change (compared with live). Absent bars indicate no significant difference between the specific affected cedar status and live forests.

affected by stand-replacing disturbances (large windthrow or logging) and minor windthrow disturbance (Deal et al. 1991), our results show that western hemlock regenerates vigorously on

plots affected by decline, and changes in community composition, as described by IVs, show a turnover to western hemlock-dominated forests. However, because our sampling frame was

restricted to plots with a total live and dead basal area of ≥ 35 m²/ha, our results are not generalizable to dynamics on poorly drained, acidic soils that may be more likely to convert to scrub forests.

Chronosequences and associated space-for-time substitutions serve as a useful tool for studying temporal dynamics of plant communities that occur across time (Oliver and Larson 1996, Fukami and Wardle 2005, Walker et al. 2010). Despite critiques as to whether there are predictable links between sites and at what rates characteristics actually change over time (Moral 2007), Walker et al. (2010) assert that chronosequences are well-suited for studying plant communities that have low biodiversity, rapid species turnover, and low frequencies and severity of disturbance. We applied this methodology to coastal temperate forests with relatively low vascular plant diversity and restricted our sites to those where widespread mortality was evident as a significant disturbance (Fig. 3), avoiding windthrow. Based on current understanding of the pathway to decline, varying snowpack conditions (Hennon et al. 2010, 2012) were likely the cause of the spatial pattern of mortality observed across the study area (Fig. 2); old mortality occurred in the more southerly plots and live further north (~110 km distance; less than 1 latitude between northernmost and southernmost plots). We acknowledge that there may have been confounding factors, such as variability in deer populations, snow conditions, or relative abundance of trees species associated with the spatial distribution, that affected the patterns we observed across the chronosequence. Specifically, seedling and sapling abundance at sites located in GLBA may have been positively affected by geographic location at the northern limit of Sitka black-tailed deer (Schoen and Kirchhoff 1990). The observed increase in volume of forage species post-decline may also have a negative feedback on yellow-cedar regeneration, as deer browsing can be a barrier to seedling performance (Hennon et al. 2006, 2008). As there were no affected forests identified in GLBA by aerial survey, plots measured increased our sample size of live forests and extended our chronosequence further north across a relatively limited spatial extent. Our biophysical controls used for site selection helped reduce the likeli-

hood of other factors driving variation in forest structure and community composition among the cedar status categories.

Understory plant community

Our study provides evidence of a dynamic understory response that occurs as forests become affected by decline. Changes in community composition were elucidated by the increase in Shannon diversity for functional groups and the dissimilarities in functional group abundance across the chronosequence (Fig. 7A): live forests were primarily differentiated by bryophyte abundance, recent mortality by graminoids, and old mortality by shrubs. We found forests affected by decline can lead to increased forage production over time, potentially increasing deer carrying capacity. As variations in snow-depth are known to effect browse availability (White et al. 2009), reduced snowpack that triggers tree mortality may also expand winter habitat for deer.

An extensive literature on widespread mortality of a single dominant tree species from other types of disturbances (e.g., insects or pathogens that target a host species) indicates that overstory loss typically alters understory plant communities (Anderegg et al. 2012). Recent studies on the effects of a species dieback associated with climate change on understory vegetation showed: increases in species richness and abundance seven years after a major drought-induced mortality event of *Juniperus monosperma* (Kane et al. 2011); shifts in community composition with decreases in herbaceous species, cover, and volume; and increases in shrub abundance, cover, and volume over a two-year time period in stands affected by sudden aspen decline (Anderegg et al. 2012). Typically characterized by frequency, duration, severity, size and spatial pattern, disturbance regimes provide critical information to understand stand formation and subsequent development (O'Hara and Ramage 2013). Timing and intensity of yellow-cedar mortality plays a critical role in determining plant community responses. Although we observed an increase in the vascular plant taxa identified across the chronosequence, our ability to make inferences to changes in species richness and diversity as forest become affected by decline was limited by taxonomic resolution (Appendix

A). We did not identify sedges (Cyperaceae), grasses (Poaceae), clubmosses (Lycopodiophyta), horsetails (*Equisetum* spp.), and bryophytes at the species level, but the abundance of the associated functional groups differed substantially across the chronosequence. As such, taxonomic richness and diversity for these vascular plant taxa and the bryophytes group would play an important role in overall dynamics of species diversity.

Implications for management, conservation, and ecosystem services

Our ability to identify and quantify the trajectories of ecological communities is important for monitoring and maintaining biodiversity, as well as other ecosystem services. Because of the remoteness and inaccessibility of the Archipelago in southeast Alaska, monitoring and active forest management, such as harvesting or planting, may occur only on a small portion of forest experiencing yellow-cedar decline (Hennon et al. 2012). We documented far-reaching effects of climate change on protected wilderness lands, affirming that areas once set-aside for conservation may be insufficient for species preservation in a changing climate (Heller and Zavaleta 2009). Given expected climate change in the current century, many vegetation types and individual species may lose representation in protected areas (Scott et al. 2002, Burns et al. 2003, Araújo et al. 2004). Effective conservation strategies require understanding the changing plant community dynamics and assessing habitat where species are more likely to survive on both managed and protected lands. Managers and conservation planners operating in other ecosystems may need to consider impacts of climate change on plant communities in protected areas to evaluate broad-scale implications of activities (such as timber harvest) on actively managed lands. Whether this species decline will expand northward into the live forests in Glacier Bay National Park and Preserve is currently unknown; this study's plots offer opportunities for directly monitoring future changes in affected and unaffected forests to date.

The changes observed across the chronosequence can have a range of cascading effects on ecosystem services. Conversion to western-hemlock dominated forests represents a long-term

reduction in culturally valued trees and a loss of the cultural services these trees provide. Forests affected by decline may sequester less carbon in the long-term, given western hemlock's relatively shorter lifespan (Klinka et al. 2000) and wood deterioration rates (Hennon et al. 2000, 2002). Researchers are just beginning to understand the influence of dead cedars on watershed nutrient export (D'Amore et al. 2009). By replacing yellow-cedar trees with the most abundant tree species in the region (western hemlock), yellow-cedar decline can lead to a loss of conifer diversity at the landscape level, yet may provide increased forage availability for deer hunted throughout the region.

Although our research occurred on protected lands at the northern reaches of yellow-cedar decline, dynamics observed can provide forest managers on the Tongass National Forest with a better understanding of the processes of stand development and conifer species most likely to dominate impacted forests over time. In consideration of salvage activity or thinning on managed lands affected by decline, our results suggest that managers should recognize that western hemlock is more likely to outcompete other species, and that favoring spruce or mountain hemlock individuals may help maintain conifer diversity. Further research could evaluate whether forests affected by decline support a greater deer population or if shifting hunting pressures to these areas could have a positive impact on yellow-cedar regeneration. Our study also underscores the importance of maintaining yellow-cedar populations at higher elevations, given the decreased likelihood for yellow-cedar regeneration once low-elevation, coastal forests become affected by the dieback.

Conclusion

Species traits, autecology, and community ecology, including overstory–understory interactions, need to be considered when examining and predicting the effects of climate change on emerging plant communities. The temporal variations we observed in regeneration, as well as changes in understory and overstory composition, highlight the importance of considering long-term effects of a species dieback associated with climate change. Short-term studies of forest development processes could lead to misinter-

pretation of long-term trajectories and impacts to diversity. In consideration of how human populations will adapt to ecosystem changes if climate-induced forest mortality accelerates into the future, a critical first step is to improve understanding of the cascading effects of these mortality events on the human-natural system. Directional ecological changes may not be unidirectional when taking into account a diversity of perspectives on ecosystem services. How people use and value the services forests provide, from material uses to intangible values, may be important factors in interpreting impacts of widespread forest mortality in the human dimension.

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SUPPLEMENTAL MATERIAL

APPENDIX A

Table A1. Common and scientific names of understory vascular plants identified in the study area.

Common name	Scientific name
Shrubs and sub-shrubs	
Sitka alder	<i>Alnus viridis</i> (Chaix) DC. subsp. <i>sinuata</i> (Regel) Á. Löve & D. Löve
Bunchberry dogwood	<i>Cornus canadensis</i> L.
Copperbush	<i>Elliottia pyroliflora</i> (Bong.) S.W. Brim & P.F. Stevens
Black crowberry	<i>Empetrum nigrum</i> L.
Alaska bellheather	<i>Harrimanella stelleriana</i> (Pall.) Coville
Alpine laurel	<i>Kalmia microphylla</i> subsp. <i>occidentalis</i> (Hook.) A. Heller (Small) Roy L. Taylor & MacBryde
Twinflower	<i>Linnaea borealis</i> L.
Rusty menziesia	<i>Menziesia ferruginea</i> Sm.
Devil's club	<i>Oplopanax horridus</i> (Sm.) Miq.
Yellow mountainheath	<i>Phyllodoce glanduliflora</i> (Hook.) Coville
Bog labrador tea	<i>Rhododendron groenlandicum</i> (Oeder) K.A. Kron & W.S. Judd
Cloudberry	<i>Rubus chamaemorus</i> L.
Strawberryleaf raspberry	<i>Rubus pedatus</i> Sm.
Salmonberry	<i>Rubus spectabilis</i> Pursh
Alaska blueberry	<i>Vaccinium alaskaense</i> Howell
Bog blueberry	<i>Vaccinium cespitosum</i> Michx.
Oval-leaf blueberry	<i>Vaccinium ovalifolium</i> Sm.
Small cranberry	<i>Vaccinium oxycoccos</i> L.
Red huckleberry	<i>Vaccinium parvifolium</i> Sm.
Dwarf alpine blueberry	<i>Vaccinium uliginosum</i> L. subsp. <i>alpinum</i> (Bigelow) Hultén
Mountain cranberry	<i>Vaccinium vitis-idaea</i> subsp. <i>minus</i> L. (Lodd.) Hultén
Ferns and lycophytes	
Subarctic ladyfern	<i>Athyrium filix-femina</i> subsp. <i>cyclosorum</i> (L.) Roth (Rupr.) C. Chr.
Deer fern	<i>Blechnum spicant</i> (L.) Sm.
Spreading woodfern	<i>Dryopteris expansa</i> (C. Presl) Fraser-Jenkins & Jermy
Horsetails	<i>Equisetum</i> spp.
Western oakfern	<i>Gymnocarpium dryopteris</i> (L.) Newman
Clubmosses	Lycopodiophyta
Licorice fern	<i>Polypodium glycyrrhiza</i> D.C. Eaton
Forbs	
Bride's feathers	<i>Aruncus dioicus</i> (Walter) Fernald
Fernleaf goldthread	<i>Coptis asplenifolia</i> Salisb.

Table A1. Continued.

Common name	Scientific name
Threeleaf goldthread	<i>Coptis trifolia</i> (L.) Salisb.
Sierra shootingstar	<i>Dodecatheon jeffreyi</i> Van Houtte
Subalpine fleabane	<i>Erigeron peregrinus</i> (Banks ex Pursh) Greene subsp. <i>peregrinus</i>
Deer cabbage	<i>Nephrophyllidium crista-galli</i> (Menzies ex Hook.) Gilg
Swamp gentian	<i>Gentiana douglasiana</i> Bong.
Heartleaf twayblade	<i>Listera cordata</i> (L.) R. Br.
Skunk cabbage	<i>Lysichiton americanus</i> Hulten & H. St. John
False lily of the valley	<i>Maianthemum dilatatum</i> (Alph. Wood) A. Nelson & J.F. Macbr.
Fringed grass of Parnassus	<i>Parnassia fimbriata</i> K.D. Koenig
Narrow beech fern	<i>Phegopteris connectilis</i> (Michx.) Watt
Scentbottle	<i>Platanthera dilatata</i> (Pursh) Lindl. ex Beck
Western rattlesnakeroot	<i>Prenanthes alata</i> (Hook.) D. Dietr.
Canadian burnet	<i>Sanguisorba canadensis</i> L.
Claspleaf twistedstalk	<i>Streptopus amplexifolius</i> (L.) DC.
Small twistedstalk	<i>Streptopus streptopoides</i> (Ledeb.) Frye & Rigg
Threeleaf foamflower	<i>Tiarella trifoliata</i> L.
Arctic starflower	<i>Trientalis europaea</i> subsp. <i>arctica</i> L. (Fisch. ex Hook.) Hulten
Green false hellebore	<i>Veratrum viride</i> Aiton
Marsh violet	<i>Viola palustris</i> L.
Graminoids	
Sedges	Cyperaceae
Grasses	Poaceae

Note: Common and scientific names listed according to the PLANTS Database (USDA, NRCS 2014); groupings were delineated first by growth habitat (shrubs and forbs) in the PLANTS Database and then further distinguished to ferns, lycophytes, and graminoids according to Pojar and MacKinnon (1994).

APPENDIX B

Table B1. Mean density of live seedlings (<10 cm height) and saplings (<2.5 cm dbh and ≥1.0 m height). Western hemlock and mountain hemlock seedlings are reported to genus.

Species	Seedlings	Saplings
Live		
Yellow-cedar	37,431	395
Hemlock		
Western		555
Mountain		115
Western + mountain	85,139	
Sitka spruce	8,194	105
Shore pine	2,014	20
All species	132,778	1,190
Recent mortality		
Yellow-cedar	11,458	45
Hemlock		
Western		968
Mountain		323
Western + mountain	126,563	
Sitka spruce	14,896	405
Shore pine	1,146	15
All species	154,063	1,755
Mid-range mortality		
Yellow-cedar	7,500	167
Hemlock		
Western		1,594
Mountain		257
Western + mountain	128,750	
Sitka spruce	12,143	450
Shore pine	2,857	13
All species	151,250	2,481

Table B1. Continued.

Species	Seedlings	Saplings
Old mortality		
Yellow-cedar	12,841	16
Hemlock		
Western		728
Mountain		302
Western + mountain	307,273	
Sitka spruce	17,386	490
Shore pine	455	8
All species	337,955	1,546

APPENDIX C

Table C1. Outputs from selected zero-inflated Poisson models used to model the probability of species' occurrence in each cedar decline status and to test for significant effect of cedar decline status on each species' abundance in sapling stage.

Model, by species	Coefficient	Odds ratio	SE	<i>p</i>
Yellow-cedar				
Binomial model				
Intercept	-0.5975		1.5247	0.6952
Recent mortality	-1.0877	0.3370	0.8383	0.1945
Mid-range mortality	-2.2793	0.1024	1.2771	0.0743
Old mortality	-2.6391	0.0714	1.1906	0.0266*
Canopy openness	0.0281		0.0496	0.5718
Poisson model				
Intercept	-2.3146		0.8472	0.0063**
Recent mortality	-2.3912		0.6727	0.0003***
Mid-range mortality	-0.5003		0.3272	0.1263
Old mortality	-0.9537		0.9397	0.3102
Canopy openness	0.1311		0.0236	0.0000***
Western hemlock				
Binomial model				
Intercept	3.3839		1.6048	0.0350*
Recent mortality	1.5985	4.9458	1.2477	0.2001
Mid-range mortality	17.9416	61,937,081.9490	3,997.8072	0.9964
Old mortality	-0.9370	0.3918	0.8726	0.2829
Canopy openness	-0.0711		0.0489	0.1460
Poisson model				
Intercept	1.6648		0.2397	0.0000***
Recent mortality	0.3049		0.1377	0.0268*
Mid-range mortality	0.6737		0.1480	0.0000***
Old mortality	0.6514		0.1430	0.0000***
Canopy openness	0.0139		0.0075	0.0625
Mountain hemlock				
Binomial model				
Intercept	-4.5966		1.7273	0.0078**
Recent mortality	0.0376	1.0383	0.8447	0.9645
Mid-range mortality	1.5762	4.8367	1.2783	0.2176
Old mortality	1.3601	3.8966	0.9285	0.1430
Canopy openness	0.1302		0.0537	0.0154*
Poisson model				
Intercept	0.7244		0.4532	0.1100
Recent mortality	0.5641		0.2727	0.0386*
Mid-range mortality	-0.2406		0.3300	0.4659
Old mortality	0.2798		0.2803	0.3182
Canopy openness	0.0178		0.0117	0.1301

Table C1. Continued.

Model, by species	Coefficient	Odds ratio	SE	<i>p</i>
Sitka spruce				
Binomial model				
Intercept	0.4623		1.4064	0.7424
Recent mortality	1.7054	5.5037	0.9510	0.0729
Mid-range mortality	1.0612	2.8897	1.0488	0.3116
Old mortality	1.5527	4.7243	0.9306	0.0952
Canopy openness	-0.0158		0.0452	0.7271
Poisson model				
Intercept	1.9574		0.4491	0.0000***
Recent mortality	1.1931		0.3036	0.0001***
Mid-range mortality	1.7485		0.3497	0.0000***
Old mortality	1.2361		0.2930	0.0000***
Canopy openness	-0.0442		0.0132	0.0008***
Shore pine				
Binomial model				
Intercept	-22.8581		9.6605	0.0180*
Recent mortality	-2.2061	0.1101	1.9900	0.2676
Mid-range mortality	-3.7034	0.0246	2.0725	0.0740
Old mortality	-7.8147	0.0004	4.1696	0.0609
Canopy openness	0.6006		0.2594	0.0206*
Poisson model				
Intercept	0.5002		34.3391	0.9884
Recent mortality	-10.5767		157.2025	0.9464
Mid-range mortality	-9.1777		110.4300	0.9338
Old mortality	-11.6812		387.9702	0.9760
Canopy openness	-0.0009		0.8761	0.9992

Notes: Data were considered as zeros versus non-zeros, and a binomial with logit link model (zero hurdle) was used to model the probability of observing a zero-value. Non-zero observations were modelled with a truncated poisson with logit link (count model). Best models were selected based upon AIC values. All models were improved by the inclusion of canopy openness as an explanatory factor.