Shifting Climate, Altered Niche, and a Dynamic Conservation Strategy for Yellow-Cedar in the North Pacific Coastal Rainforest

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The extensive mortality of yellow-cedar along more than 1000 kilometers of the northern Pacific coast of North America serves as a leading example of climate effects on a forest tree species. In this article, we document our approaches to resolving the causes of tree death, which we explain as a cascade of interacting topographic, forest-structure, and microclimate factors that act on a unique vulnerability of yellow-cedar to fine-root freezing. The complex causes of tree mortality are reduced to two risk factors—snow depth and soil drainage—which are then used to model present and future cedar habitat suitability. We propose a dynamic, comprehensive conservation strategy for this valuable species on the basis of zones created by shifting climate, cedar's ecological niche, and observed risk factors. Research on yellow-cedar decline is offered as a template for understanding and adapting to climate change for other climate–forest issues.

Keywords: climate adaptation, forest decline, root cold tolerance, Callitropsis nootkatensis, Chamaecyparis nootkatensis

Climate change presents considerable challenges to scientists, policymakers, and forest managers concerned with the conservation and management of the world's forests, which support the health and productivity of biological systems and provide a wealth of ecosystem services. Climate is the primary driver that shapes the distribution and abundance of forest trees, as is demonstrated by contemporary relationships as well as paleoecological records (Woodward 1987, Davis and Shaw 2001). Climate influences vegetation patterns broadly as the geographic expansion and contraction of species' ranges are affected by processes of dispersal and mortality (Neilson 1986). Given the dynamic nature of climate and its effects on forests, new views are emerging on long-standing strategies for conservation and restoration that were previously developed with an assumption of a static or gradually changing climate (Millar et al. 2007).

An altered climate can place considerable stress on forest trees and may result in widespread tree death, yet there are few well-documented examples of how this develops in forest ecosystems. A forest's responses to climate change may appear as visible, extensive tree death expressed as forest declines (Sturrock et al. 2011) and insect outbreaks (Benz et al. 2010), or they may be detected in more subtle forms, such as changes in tree competitiveness and reproduction that gradually affect the forest's species composition. Teasing apart climate-induced change from natural forest dynamics and the action of endemic biotic agents in forest health issues has proven difficult and requires a multifaceted research approach. For example, it is possible to quantify the rates of forest change with repeat surveys, such as the recent elevated death rates of old trees in the western United States (van Mantgem et al. 2009) and the upward elevational shifts of plant species during the twentieth century in Western Europe (Lenoir et al. 2008), but without supporting mechanistic research, findings from such studies lead to speculation about the causal roles of climate. To complicate matters, stress and tree death are typically monitored over short periods of time, which makes it difficult to distinguish any causal roles among weather, normal decadal oscillations (e.g., the El Niño–Southern Oscillation, the Pacific Decadal Oscillation), and true longer-term climate deviations (IPCC 2007). Long-lived tree species must endure all of these forms of climate variation.

There is considerable uncertainty and speculation about the function of climate in broad-scale forest-health issues. We suggest that climate plays some role in most instances of widespread tree mortality but also that climate would likely not act alone as a causal factor. A more-complete

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understanding of the causes of tree stress or death integrated with unique species' vulnerabilities is needed in order to place the role of climate in perspective. Given the uncertainties about climate change and its effects on forest ecosystems, policymakers and forest managers are reluctant to make decisions or to use resources to implement adaptation measures for forest conservation and management. We contend that more systematic investigations that produce well-documented explanations of climate effects on forest ecosystems are needed in order to build the necessary confidence for policymakers and forest managers to intervene. Furthermore, key environmental factors that interact with climate to compromise tree health and to initiate tree mortality need to be better understood and incorporated into any conservation plans designed for adaptation to climate change.

In this article, we outline our understanding of the interaction of climate with other key environmental factors that has caused an extensive forest decline of yellow-cedar (*Callitropsis nootkatensis* [D. Don] D.P. Little; figure 1). We draw on 30 years of research on yellow-cedar decline, which provides a template for an integrated research program in which vegetation's response to climate change is examined. We combine this knowledge with information about the ecological niche of yellow-cedar and the forest-decline risk factors to develop a framework for an adaptive broad-scale conservation strategy for the species. This uniquely comprehensive research approach applied to yellow-cedar may serve as a case study for understanding the potential decline and conservation of other tree species.

Figure 1. Yellow-cedar in West Chichagof–Yakobi Wilderness Area, a pristine area of coastal Alaska, faces intensive mortality. Photograph: Paul E. Hennon.

Yellow-cedar and its decline

Yellow-cedar is an ecologically, culturally, and economically important tree species in the coastal temperate rainforests of Alaska and British Columbia. This defensive, slow-growing tree has few natural insect and disease agents and is capable of great longevity of more than 1000 years (Harris 1990). Yellow-cedar wood and bark have been of long-standing importance to the area's indigenous people for a number of domestic uses, including shelter, clothing, canoe paddles, and totem poles (Turner 1998). The wood has great commercial value because of its desirable strength and decay-resistance properties. Yellow-cedar is limited to high elevations throughout most of its range, especially in the southern portion, which extends to the California–Oregon border. To the north, especially in Alaska, yellow-cedar grows from sea level to near timberline (Harris 1990). Locally, its niche is strongly controlled by an affinity for wet soils (Krajina 1969, Neiland 1971). It is in these northern locales that the extensive mortality known as *yellow-cedar decline* occurs (figure 1).

Yellow-cedar decline occurs in several thousand locations of concentrated mortality, totaling approximately 200,000 hectares in southeast Alaska (figure 2, inset map). Another 50,000 hectares extend into adjacent British Columbia (Hennon et al. 2005, Westfall and Ebata 2009). Ground-based plots reveal the intensity of tree death; approximately 70% of the mature yellow-cedar trees are dead in these declining forests (Hennon et al. 1990a, D'Amore and Hennon 2006), but some areas experience nearly complete mortality (figure 1). Most of the tree death is on wet soils (Johnson and Wilcock 2002) where, paradoxically, yellow-cedar was previously well adapted and competitive (Neiland 1971, Hennon et al. 1990a). Affected stands are typically composed of long-dead, recently dead, dying, and some surviving trees, which suggests that mortality is long term and continuing.

Initial approaches to determine the origins of tree death

The cause of yellow-cedar death was perplexing for many years. The phenomenon was initially evaluated by a small team of tree pathologists who examined the roots, boles, and crowns of trees in varying stages of dying to establish a sequence of symptom development (Hennon et al. 1990b). Fine-root death was found to be the initial symptom, followed by coarse-root death, necrotic cambial bole lesions and crown dieback, with distal foliage the last to

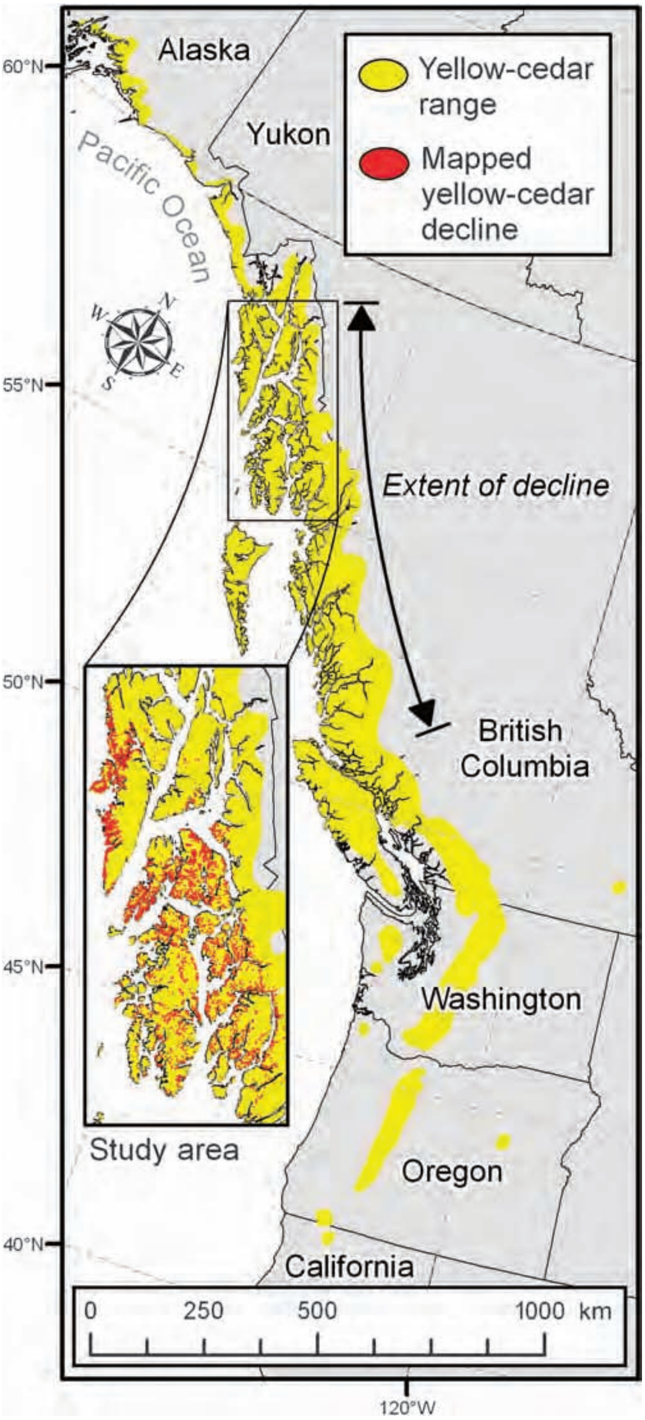

Figure 2. Natural distribution of yellow-cedar (Little 1971), latitudinal extent of decline covering approximately 1000 kilometers (km), and decline on 200,000 hectares in southeast Alaska (inset), mapped by aerial survey.

die (Hennon et al. 1990b). Organisms were collected or isolated from symptomatic tissues, but each was eventually ruled out as a causal agent by inoculation studies on cedars or by the lack of consistent association with tree death in forests. Some of these potential agents played secondary roles in yellow-cedar mortality, but higher fungi (Hennon et al. 1990b), oomycetes (Hansen et al. 1988), insects (Shaw et al. 1985), nematodes (Hennon et al. 1986), and viruses and mycoplasmas (Hennon and McWilliams 1999) were dismissed as initiating the decline. This deductive approach produced mainly negative results and indicated that a biotic agent was not the primary cause of tree death.

We assimilated temporal and spatial clues about the timing of decline onset and perpetuation and about the pattern of mortality across the landscape. The extreme decay resistance of yellow-cedar wood (Kelsey et al. 2005) results in dead trees' standing long after death and produces a standing record that allows the reconstruction of annual mortality rates back through the 1880s (Hennon et al. 1990c, Stan et al. 2011). Elevated yellow-cedar mortality began around 1880–1900 and continued through the 1900s, with peak values in the 1970s and 1980s (Hennon and Shaw 1994). The oldest record represented the original wave of mortality, and many of these trees were still standing more than 100 years after death (Hennon et al. 1990c). Some patches of decline exhibited patterns of local spread (around 100 meters) in the last century along a hydrologic or slope gradient, with long-dead trees in central areas with poorly drained soils and more recently killed or dying trees around the periphery on sites with better drainage (Hennon et al. 1990a).

We can draw several conclusions from these early studies: The problem appears unique to yellow-cedar, mortality starts with fine roots, yellow-cedar decline began about 100 years ago but increased more recently, decline is typically predisposed on poorly drained soils, and the direct cause of decline appears to be some form of abiotic injury rather than a pathogen or other organism. Therefore, the range of possible direct causes had been narrowed in 1997 in the synthesis paper "What is killing the trees?" by Hennon and Shaw (1997), but the basic question remained unresolved. Next, we broadened our scope to study abiotic factors, such as hydrology, soil temperature and chemistry, and microclimate. In a risk-factor analysis, we compared the values of these abiotic factors with the health of yellow-cedar forests in two watersheds and clarified that greater extremes in seasonal air and soil temperature were consistently associated with dead trees (D'Amore and Hennon 2006). These findings, along with cumulative knowledge from the symptoms of dying trees and clues from temporal and spatial patterns of decline, suggested a hypothetical pathway of indirect factors leading to root-freezing injury as the proximate cause of tree death (figure 3).

Interdisciplinary research to evaluate the complex of causal factors

The tree-injury pathway, with its interrelated factors (figure 3), was too complex to be assessed in a single study; therefore, it became the framework for our research program and guided the execution of studies in an attempt to resolve the cause of yellow-cedar decline. Interactions along the pathway were addressed with one or more studies on

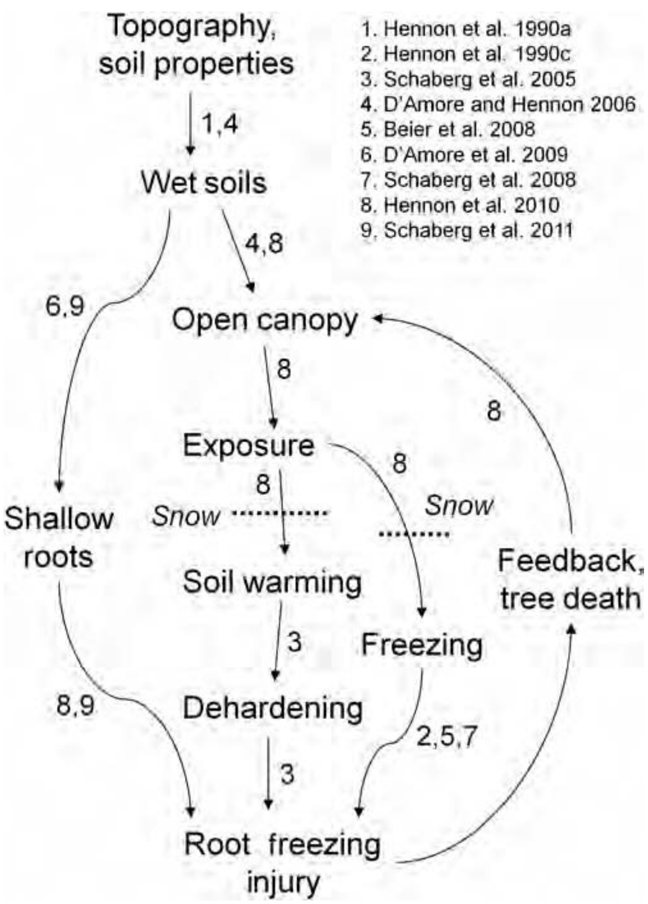

Figure 3. Cascading factors that contribute to yellow-cedar decline, culminating in fine-root mortality and tree death. The mitigating role of snow cover is shown. Tree death is a feedback that can expose adjacent trees to greater fluctuation in microclimate, thereby creating conditions for local spread of this forest decline. Numbers refer to studies on interacting factors.

hydrology, canopy cover, air and soil temperatures, snow, yellow-cedar phenology, or freezing injury to seedlings and mature trees (figure 3). We attempted to answer two general questions related to cedar decline while conducting the specific studies: What is the unique physiological vulnerability of yellow-cedar, and what change in the environment triggered this mortality?

Forest species composition and productivity in north coastal temperate rainforests are tightly controlled by soil drainage (Neiland 1971). The optimal niche for yellow-cedar is in soils with intermediate drainage, but it can occupy sites that experience a wide range of soil-saturation levels (figure 4; Hennon et al. 1990a). Yellow-cedar can grow well when it is established on better-drained, nutrient-rich sites (D'Amore and Hennon 2006), but it is frequently outcompeted there, most commonly by western hemlock (*Tsuga heterophylla* [Raf.] Sarg.). The decline of yellow-cedar is associated with the wetter side of the drainage gradient, and there is an apparent threshold that separates live and dead forests (figure 4). We interpret this as meaning that yellow-cedar's niche is compromised on sites with poor and moderate drainage.

Wet soils limit nutrient cycling and rooting depth, which inhibits tree growth rates and thereby reduces the canopy cover and standing biomass of live trees (D'Amore and Hennon 2006). The size and age structure of existing trees (Hennon and Shaw 1994, Beier et al. 2008) suggest that these wet soil conditions were probably present before the initiation of yellow-cedar decline around 1880–1900, and may have been established several thousand years ago, when the climate along the Pacific coast became cool and wet, which led to extensive peatland development (Heusser 1960). We estimated forest canopy cover using both hemispherical photographs from the ground and LIDAR (light detection and ranging) remote sensing from the air. Cover varied greatly, from none in bogs to over 89% in upland forests, and was highly correlated with the basal area of live trees for all species along the drainage gradient (Hennon et al. 2010).

Initially, we presumed that yellow-cedar trees had abundant roots in shallow horizons of wet soils as a response to anoxia (i.e., roots do not survive in soils that are consistently saturated with water), but evidence from foliar-nutrient concentrations raised the question of the nutrient-acquisition strategies employed by cedars to maintain growth in a nutrient-limited environment (i.e., wet soils). We proposed an adaptation such that cedars rely on the linked uptake of nitrate anions with calcium cations to exploit shallow, rich sources of nitrogen (D'Amore et al. 2009). A nutritional analysis of the foliage also indicated that yellow-cedar takes up more calcium (concentrated in upper organic soil horizons) and less aluminum (concentrated in deeper mineral horizons) than other sympatric conifers, which supports the possibility that yellow-cedar has a greater proportion of shallow fine roots than many of its competitors (Schaberg et al. 2011). Along with anoxia, this adaptation for enhanced nitrate uptake leads to shallow rooting and predisposes yellow-cedar to an increased risk of injury from near-surface soil-temperature fluctuations.

Seasonal air and soil temperatures in forests are influenced by canopy cover. Dense canopies intercept solar energy and buffer the areas below the canopy from high temperatures through shading. This cover also traps heat that emanates from the ground, which leads to temperature inversions below the canopy during cold weather. Forests with less canopy cover experience warmer daily maximum and colder daily minimum air-temperature values, and these canopy effects on daily temperature ranges are most pronounced in the spring months (D'Amore and Hennon 2006). Temperature variability in soils is inversely related to soil depth. In the deeper rooting zone (15-centimeter [cm] depth), we found greater late-winter and spring warming in areas with less tree canopy, but only infrequent freezing (D'Amore and Hennon 2006). The shallow rooting zone (7.5-cm depth), however, showed more pronounced diurnal temperature

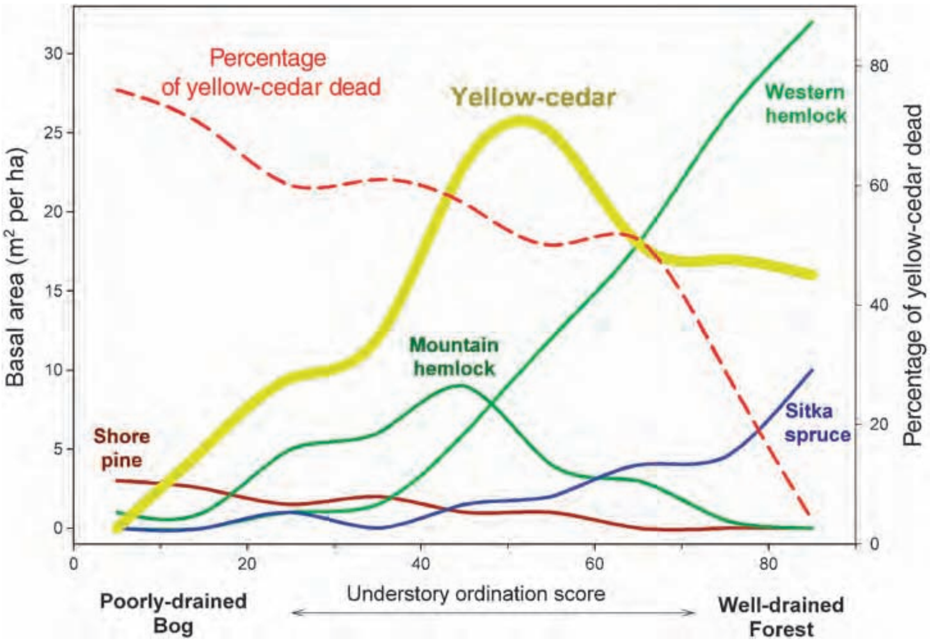

Figure 4. Yellow-cedar's optimum edaphic niche and the occurrence of yellow-cedar mortality along the soil-drainage gradient. The abundance (live basal area) of yellow-cedar and competing tree species was determined by splining the midpoint values from nine intervals along a range of soil-drainage levels indicated by understory plant composition (expressed with ordination scores) from 280 plots (Hennon et al. 1990a). **Ordination** *is a multivariate statistical technique used to examine gradients in species-rich datasets. The percentage of dead yellow-cedar basal area reveals an apparent threshold of drainage, beyond which yellow-cedar is healthy but outcompeted by faster-growing tree species. Abbreviations: ha, hectare; m², square meters.*

variation, even greater warming effect with less canopy, and frequent subfreezing temperatures (Hennon et al. 2010), as mentioned below.

A series of measurements in the field and an experimental project revealed the link between cold tolerance and freezing injury in yellow-cedar trees. Although the results of past work (e.g., those of Hawkins et al. 2001) suggested that yellow-cedar has limited cold hardiness, the influence of cold tolerance on yellow-cedar decline had never been examined. We evaluated the seasonal differences in cold tolerance of mature yellow-cedar and western hemlock trees at a site affected by decline (Schaberg et al. 2005). Using foliar cold tolerance as a surrogate for root cold tolerance because the two measurements are seasonally parallel (Sakai and Larcher 1987), we documented two patterns that are consistent with our proposed decline scenario (figure 3): (1) In the spring, yellow-cedar trees dehardened almost 13 degrees Celsius (°C) more than did western hemlock, causing yellow-cedar to be more vulnerable to freezing injury, and (2) low- and mid-elevation stands (where decline predominates) were more vulnerable to early dehardening and subsequent freezing injury (Schaberg et al. 2005). The proposed decline mechanism was more directly tested by examining the influence of simulated snow cover on the cold tolerance and freezing injury of yellow-cedar seedlings (Schaberg et al. 2008). The roots of all seedlings were tolerant only to about –5°C, so when soil temperatures fell below this threshold on plots without simulated snow, roots were severely injured and seedlings died (Schaberg et al. 2008). Importantly, the progression of injury followed the sequences of symptoms for mature trees documented in the field, starting with root mortality in the winter and early spring, then foliar damage, and eventually whole-plant mortality when the injured roots were incapable of supplying the foliage with water and other resources (Hennon et al. 1990b). We tested the hypothesis that yellow-cedar had unique freezing vulnerability by measuring the fine-root cold hardiness of yellow-cedar and four other sympatric conifers growing together in a mixed stand from the fall to the spring (Schaberg et al. 2011). Across all dates, yellow-cedar roots were less cold tolerant than those of the other species (Schaberg et al. 2011). Although all of the species reached their maximum hardiness levels in January, yellow-cedar's winter hardiness was minimal then (the roots showed significant injury at approximately –6°C), and roots fully dehardened by March. The limited hardiness and high baseline cellular membrane leakage of yellow-cedar roots (Schaberg et al. 2011), combined with other measures of photosynthesis (Grossnickle and Russell 2006) and root growth (Arnott et al. 1993), suggest that yellow-cedar is poised for physiological activity when suitable environmental conditions occur (e.g., allowing for nitrate uptake when snowpack melts; D'Amore et al. 2009). Whatever the reasons for its unique physiology, the results indicate that yellow-cedar roots are shallower and less cold tolerant than those of other associated conifers and, therefore, are more vulnerable to injury from superficial soil freezing.

Snow is an effective insulator for soils, and it buffers soil temperatures at the threshold between freezing and thawed conditions. The soil temperatures that we monitored in the shallow-rooting zone (7.5-cm depth) frequently dropped below the lethal values (i.e., below –5°C) in the winter and early spring, but only when snow was not present (Hennon et al. 2010). Shallow soils covered by snow during cold-weather events usually maintained temperatures just above freezing. We suspect that the persistence of snow beyond the last hard freeze in the spring provides protection for yellow-cedars from root injury and that this explains the broad spatial distribution of yellow-cedar decline on the landscape (Hennon et al. 2008). In addition to this extensive geographic pattern of decline, mortality-induced changes in microclimate may help spread decline at the local-stand scale. Canopy cover was historically controlled by hydrology (i.e., open canopies on wetter soils; D'Amore and Hennon 2006), but a mortality-caused feedback further opens the canopy when trees die, which increases the exposure of neighboring trees (figure 3) and the resulting extremes in microclimate (Hennon et al. 2010). These areas are typically at the leading edge of tree mortality on better-drained soils, where we have documented moving fronts of dying trees (Hennon et al. 1990a).

The spatial and temporal aspects of climate-induced change

Our analysis of dead and dying yellow-cedar forests at multiple spatial scales helped us to form and evaluate the hypothesis on the cause of yellow-cedar decline. Each of three spatial scales offered a unique interpretation on the associations between decline and particular climate, landscape, site, or microsite features. At the broad scale, yellow-cedar decline has elevational limits that vary by latitude (Lamb and Winton 2011) in a manner consistent with climate controls. Decline at southern latitudes in British Columbia occurs considerably higher in elevation (i.e., 200–700 m; Hennon et al. 2005, Westfall and Ebata 2009, Wooton and Klinkenberg 2011). Along northern latitudes, decline is found at lower elevations, until finally, at the northern extent, 57.6 degrees north (°N) in Alaska, tree death is expressed in a narrow, low-elevation band from sea level to only 150 m. Snow is the proximal factor that probably controls this pattern. Maps of yellow-cedar decline and a regional snow-accumulation model in southeast Alaska show a pattern of close alignment of decline with the lowest of four snow zones (Hennon et al. 2008). Beier and colleagues (2008) quantified this relationship as 79% and 94% of yellow-cedar decline occurring in the low- and low-to-moderate-snow zones, respectively. Yellow-cedar forests appear healthy in areas that have higher levels of annual snow accumulation in Alaska, such as the northeast portions of the panhandle and Prince William Sound (Hennon and Trummer 2001).

At a middle spatial scale, we evaluated the association of decline with topographic features, including slope, aspect, and elevation. High-resolution maps of yellow-cedar decline for selected areas were produced by digitizing polygons of tree mortality as they were observed on color infrared photographs. Mount Edgecumbe, near Sitka, Alaska, is a dormant volcano with radial symmetry and gradual slopes that support open-canopy forests with abundant yellow-cedar extending from sea level to close to the timberline, at approximately 600 m. We found decline to have elevational limits there that corresponded to aspect, and decline occurred farther upslope on southerly than on northerly aspects. Detailed snow-accumulation models in which an elevational adjustment was used (Wang et al. 2005) for Mount Edgecumbe revealed the threshold of estimated annual snowfall—about 250 millimeters of annual precipitation as snow—that distinguishes the dying and healthy yellow-cedar forests (figure 5). This value is displayed for historic models built from weather-station data inputs and future projections from a conservative global circulation model. The resulting map (figure 5) indicates the changing snow conditions on Mount Edgecumbe and a future forecast in which snow accumulation adequate to protect superficial roots from freezing injury occurs only near the top of the mountain by the year 2080.

At a fine scale, the variation of site and forest conditions over the local areas of a landscape was studied using a grid of ground-based vegetation plots in two watersheds near the northern limit of yellow-cedar decline (D'Amore and Hennon 2006). It was at this local scale that yellow-cedar health could be associated with hydrology, canopy cover, microclimate, and snow in order to reveal and test causal factors. We learned that yellow-cedar was dead and dying in low-elevation areas with poor drainage, where shallow-soil temperatures were frequently below the –5°C threshold for fine-root mortality, but was healthy on wet soils further upslope, where snow insulated the roots, and on adjacent well-drained soils, where roots are deeper (figure 6; Hennon et al. 2010).

What change in the environment triggered tree death in previously healthy forests? A chronology of the natural history of yellow-cedar helps put forest decline into temporal context. The location of Pleistocene refugia (Carrara et al. 2007) aligns with the current distribution of yellow-cedar in Alaska in a manner that indicates that existing yellow-cedar populations may have origins in these refugia. An ongoing population-genetics study will address this hypothesis for yellow-cedar. Climate reconstruction through pollen analysis suggests that only in the late Holocene has coastal Alaska experienced the cool, wet climate that led to the extensive peatland vegetation (Heusser 1960) favorable for yellow-cedar expansion—the same soil conditions that subsequently became a long-term predisposing factor in forest decline (figure 3). At one location near Petersburg, Alaska, cedar pollen became abundant about 2200 years ago (Ager et al. 2010). The Little Ice Age (c. 1200–1900 CE) was a period when the majority of the glaciers in coastal Alaska reached their maximum extensions since the end of the Pleistocene (Calkin et al. 2000), but it is not known whether these glacier advances were driven by colder temperatures or by more snowfall. The ages of mature yellow-cedar trees, whether they are dead or still living, indicate that most of them regenerated and grew to their canopy status in existing forests during the Little Ice Age (Hennon and Shaw 1994, Beier et al. 2008). We hypothesize that this favorable climate

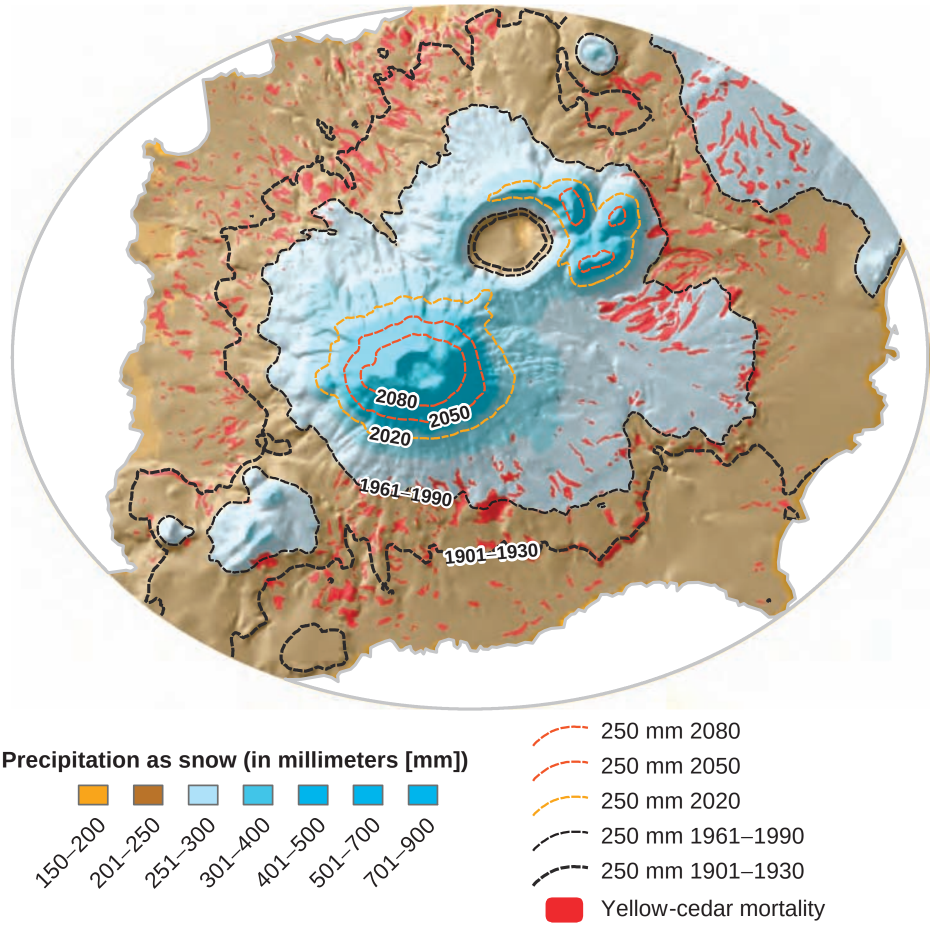

Figure 5. Mount Edgecumbe, a dormant volcano near Sitka, Alaska. The distribution of yellow-cedar decline, mapped from 1998 color infrared photography (red), and the annual precipitation as snow between 1961 and 1990 are shown. Snow cover was modeled from PRISM (Oregon State University) and downscaled using the Wang and colleagues (2005) elevation adjustment with colors indicating the values above (blue) or below (brown) the threshold of 250 millimeters of annual precipitation as snow. The historic occurrence of this modeled snow threshold is from weather station data; the future forecasts use a conservative global-circulation model (the coupled global climate model, second generation, B2 variant).

allowed yellow-cedar to regenerate prolifically—in part, because snow keeps populations of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) in check (White et al. 2009) and because deer are major herbivores of cedar seedlings. It was during the Little Ice Age that yellow-cedar became more abundant at lower elevations, where it would later be most vulnerable to decline.

The onset of yellow-cedar decline coincided with the end of the Little Ice Age (Hennon et al. 1990c), which would be consistent with reduced snow's being the environmental change that triggered widespread yellow-cedar tree death. A large pulse of yellow-cedar mortality occurred in the 1970s and 1980s (Hennon and Shaw 1994) during a notably warm period of the Pacific Decadal Oscillation (Mantua 2011). In an analysis of twentieth-century weather in southeast Alaska, Beier and colleagues (2008) reported warmer weather in the late winter and early spring, reduced snow, and a persistence of cold events in the spring—all conditions that are consistent with our interpretation of yellow-cedar decline.

When ecosystems cross a climate threshold. The forests of coastal Alaska are expected to experience the largest twenty-first-century increase in frost-free days anywhere in North America (Meehl et al. 2004) as the winter climate moves across the snow–rain threshold. Temperatures averaged near freezing during the winter months of the twentieth century at weather stations located near sea level in southeast Alaska (Beier et al. 2008). With heavy year-round precipitation, this near-freezing winter-temperature regime suggests that modest warming would dramatically reduce snow accumulation. Although the regional climate warms and less snow accumulates, the close proximity of southeast Alaska to the mainland continental climate in adjacent British Columbia and Yukon Territory allows cold air to be pushed over cedar forests during high-pressure weather events that are periodically present every spring. This juxtaposition of climates produces mild maritime weather that maintains yellow-cedar's physiological activity and reduces snow but also allows for periodic infiltration of cold continental conditions that inflict injury. Overall, the cause of yellow-cedar decline is influenced by climate that encouraged shallow rooting that was historically protected by snowpack, that more recently produced frequent warming in the winter that favored limited cold hardening, and that reduced the protection of roots by snow. Shorter-term climate decadal oscillations exacerbate these latter two effects, which leads to pulses of mortality, such as that in the 1970s and 1980s. Individual cold-weather periods in the spring with the potential to cause proximal injury continue to be frequent events, even in a warming climate.

The need for a dynamic conservation strategy

A conservation strategy for a climate-sensitive species needs to consider the manner in which past, current, and future climates affect the various ecological traits and life stages of

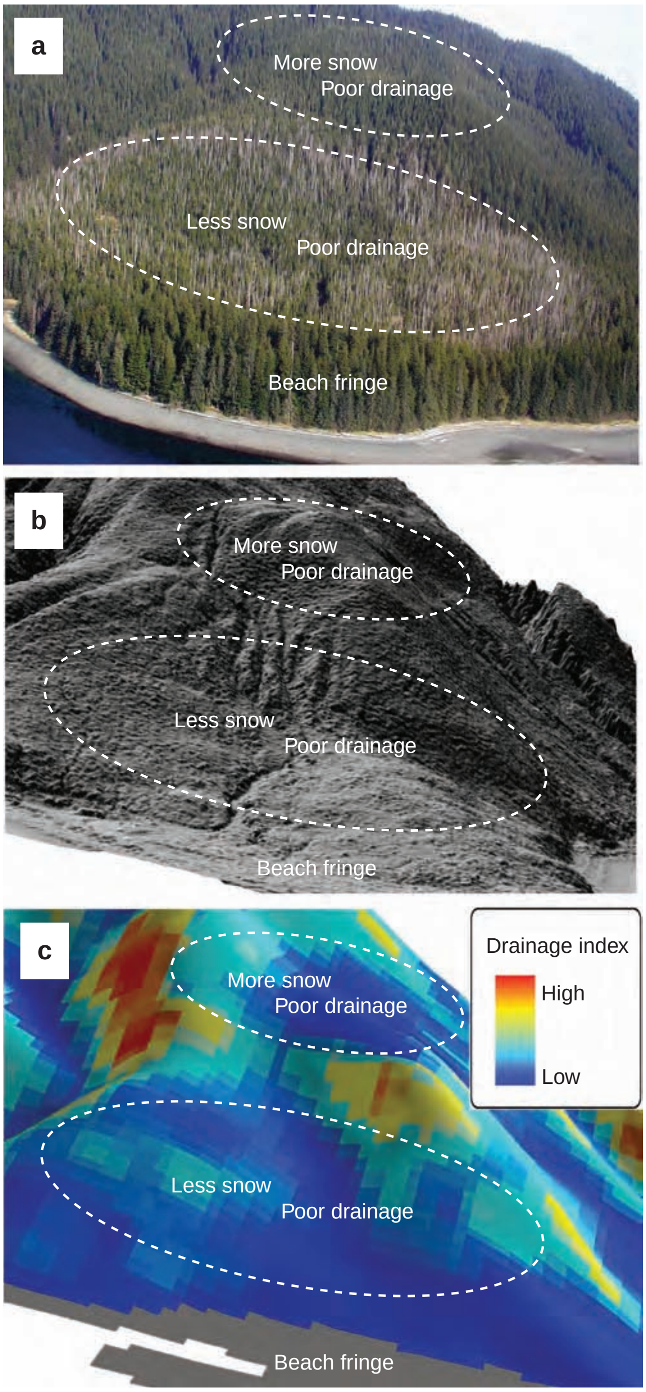

Figure 6. (a) Patch of dead and dying yellow-cedar and the surrounding forest. (b) LIDAR (light detection and ranging)–derived high-resolution digital elevation terrain model. (c) Drainage classes at Poison Cove watershed, Chichagof Island, Alaska. Yellow-cedar has died in the less-snow, poor-drainage area, but trees remain alive in the more-snow, poor-drainage area at a slightly higher elevation that has evidence of snowpack persisting later in the spring, which protects shallow roots from freezing injury (Hennon et al. 2010). Photograph: Paul E. Hennon.

that species. Because climate changes through time, the adaptive range of species becomes a moving target, and a conservation strategy must be dynamic. Climate is expected to impact each tree species in a unique manner; therefore, there is a need to model each species individually (Iverson et al. 2008).

Search for suitable yellow-cedar habitat. Modeling habitat often employs one of two approaches: Climate variables are simply correlated with a species' distribution, or a more mechanistic method using specific climate variables known to act on the species' responses of regeneration, growth, and mortality is developed (Pearson and Dawson 2003). Yellow-cedar's incomplete occupancy of suitable habitat over large geographic areas in Alaska (see the Migration zone section below) suggests that the first modeling method would be problematic. More important, our mechanistic knowledge of yellow-cedar's response to climate allows us to use specific risk factors that lead to yellow-cedar decline as a means of identifying current and future suitable and unsuitable habitat. The complex cause of yellow-cedar decline (figure 3) can be reduced to two factors for landscape modeling: snow cover and drainage. Both factors appear to have had major controls over the species composition and productivity of coastal temperate rainforests, and both are important niche factors for yellow-cedar.

Snow is a dynamic broad-scale factor used in climate-envelope modeling and is strongly associated with patterns of yellow-cedar occurrence by latitude and elevation. Soil drainage is a fine-scale factor that controls the competitive status of yellow-cedar relative to other tree species. Changes in both snow cover and soil drainage are risk factors for decline. Interestingly, both snow cover and drainage also influence the regeneration niche for yellow-cedar: Snow may limit winter browsing by deer that can devastate cedar regeneration, and the ratio of sexual to asexual reproduction appears to vary as a function of drainage in upland and bog settings (Hennon et al. 1990a).

Our conceptual approach is to integrate snow cover and drainage in order to identify unsuitable, suitable, and potential new habitats for yellow-cedar. Specifically, we nested soil drainage within favorable climate envelopes, with an emphasis on adequate snow-cover levels, to define habitat suitability as the foundation for a conservation and management strategy for yellow-cedar (figure 7). Yellow-cedar had reached its greatest competitive advantage in poorly and moderately drained soils but is now only healthy at these sites where snow-cover levels are adequate to offer protection. Within zones in which the level of snow cover is insufficient, yellow-cedar's niche has been limited to better-drained soils where its roots can penetrate deeper soil horizons (the lower zone in figure 7). The species can be expected to be less abundant in these zones unless active forest management practices favor it over competing tree species. Where snow cover is still adequate (the upper two zones in figure 7), yellow-cedar's full edaphic niche, including the portions on wet soils, is still available.

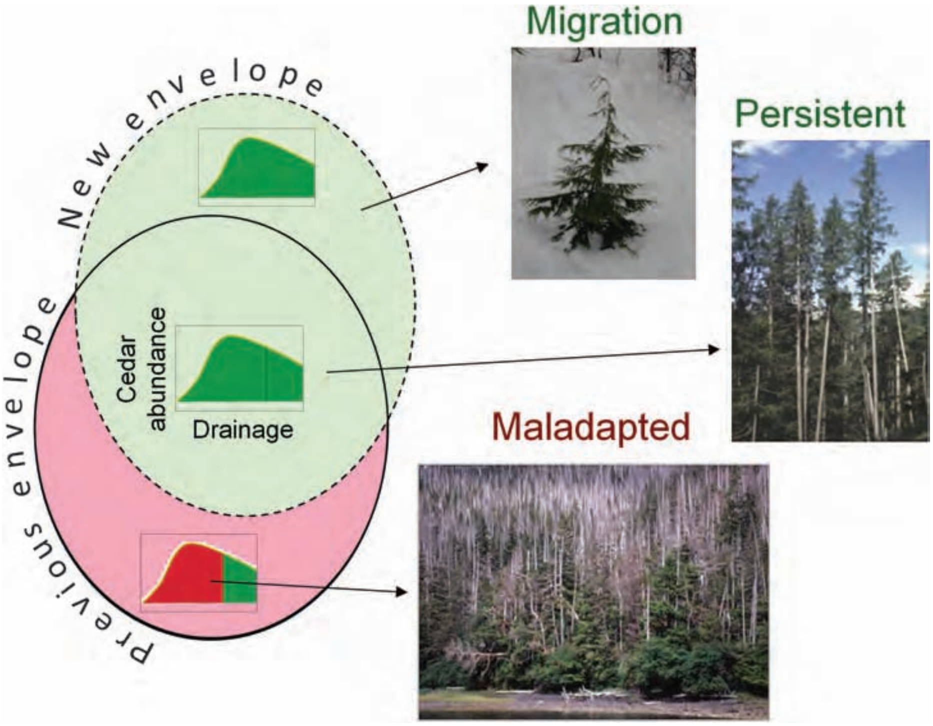

Figure 7. Conceptual diagram used to interpret the effects of climate change on the health and conservation of a forest tree species. In this article, we consider shifting climate and, more specifically, altered snow-cover zones: a zone in which yellow-cedar occurs but is no longer suited to the recent climate (maladapted), a zone in which yellow-cedar occurs and is suited to today's climate (persistent), and new areas in which yellow-cedar does not yet exist but where it would be suited if it dispersed or were planted there (migration). Snow interacts with specific yellow-cedar niche characteristics—in this case, soil drainage (see figure 4), shown here embedded in the three climate zones in order to define suitable habitat. Yellow-cedar's entire edaphic niche is available where snow is protective (the top two zones), but, where snow cover is inadequate (the lower zone), suitable habitat is only available in well-drained soils. Photograph: Paul E. Hennon.

The threshold values of both drainage and snow cover appear to control the health of yellow-cedar forests (figures 4 and 5, respectively). The snow-cover threshold—approximately 250 millimeters of annual precipitation as snow—established from our preliminary analysis can be incorporated into future scenarios as a dynamic factor. Drainage modeling can replace the proxy gradient of understory plant flora to provide a risk factor related to a threshold value for water-table depth (figure 4). Therefore, we have identified dynamic maladaptated, persistent, and migration zones. Below, we offer guidance and options to policymakers and forest managers for conservation and management in each of these zones.

The maladaptation zone: Species conversions, timber salvage, and conservation on limited suitable habitats. Given the different ecological traits among different species, climate change will probably not cause entire plant communities to shift en masse to favorable habitat. A more likely scenario is that new assemblages will appear (Webb and Bartlein 1992) as vulnerable species drop out of existing ecosystems, resident species will become more competitive, and new species will arrive through migration. Because of the remoteness and inaccessibility of the relatively unroaded island archipelago, active forest management will occur on only a small portion of the landscape with yellow-cedar decline in British Columbia and Alaska. Therefore, patterns of natural succession are of considerable interest where yellow-cedar has died, because they indicate the future composition and structure of these affected forests and their ability to meet the broad goals of biodiversity and other ecosystem services. Monitoring changes in tree species is under way to evaluate any response in the regeneration and growth of western hemlock, mountain hemlock (*Tsuga mertensiana* [Bong.] Carrière), and shore pine (*Pinus contorta* Douglas ex Loudon var. *contorta*).

One species that might substitute for yellow-cedar in the maladapted zone is western redcedar (*Thuja plicata* [Donn ex D. Don]), which grows in some of the declining yellow-cedar forests at lower elevations in Alaska and British Columbia, south of latitude 57° N. Western redcedar is a calcium-accumulating, decay-resistant, long-lived tree of commercial value that is prized by the local indigenous people. Its bark and wood properties, including wood chemistry, differ from yellow-cedar's, but the two trees have some ecological redundancy and offer similar ecosystem services. The northern range extent and elevational limit of western redcedar suggest that future warmer climate conditions will favor this tree in Alaska, which also appears to be the case in coastal British Columbia (Hamann and Wang 2006). More knowledge is needed on redcedar's adaptation to the same freezing injury that afflicts yellow-cedar before intensive efforts of promoting redcedar in declining forests would be justified (Schaberg et al. 2011).

Although species changes in the maladapted zone are likely, dead yellow-cedars may themselves have a role in management here. The large extent of yellow-cedar decline suggests an opportunity for capturing economic value from dead trees through salvage harvesting. We evaluated the value of wood from dead yellow-cedars by comparing the properties of wood from live trees with those of dead trees in five stages of deterioration. For trees dead up to 30 years, wood volume and grade recovery (Hennon et al. 2000), decay resistance (Hennon et al. 2007), and concentration of heartwood chemicals (Kelsey et al. 2005) were all comparable to those of wood from live trees. Remarkably, all strength properties were retained in wood from trees dead 80 years (Green et al. 2002). The dead yellow-cedar forests represent an astonishingly valuable wood resource for salvage. Shifting a portion of timber logging to dead yellow-cedar forests could divert some harvest away from forests that contain healthy yellow-cedar on suitable habitat.

Whatever management regime is undertaken in this zone, it is important to recognize the futility of conserving or restoring yellow-cedar where it is maladapted. Conservation areas are often established to protect biodiversity, sensitive species, and wildlife habitat. Traditionally, protection through land designation was done under the premise that forest ecosystems are somewhat static or that they may be large enough to absorb disturbance events (Millar et al. 2007). The US Forest Service developed an integrated old-growth conservation strategy of large, medium, and small reserves to protect and maintain old-growth habitat in southeast Alaska, with the goal of maintaining the mix of habitats at different spatial scales capable of supporting the full range of naturally occurring flora, fauna, and ecological processes (USFS 2008). Because of the dramatic and unexpected losses of yellow-cedar populations in protected landscapes, yellow-cedar decline serves as an example of the need to incorporate shifting climate in conservation planning. When there is sufficient knowledge of a species' responses to climate change, such as the case of yellow-cedar and its forest decline, climate and landscape models can be used to evaluate how well specific conservation areas may meet their goals in the future and where widespread problems might develop to compromise those values. Similarly, a species' response to climate forecasts should be evaluated to determine areas of maladaptation before restoration practices are implemented.

The persistent zone: Conservation and active management in occupied suitable habitat. Modeling snow accumulation into the future helps predict which areas of existing healthy yellow-cedar may be protected by snow, and which are expected to experience elevated mortality. Current and short-term future suitable habitat in high-elevation forests and those in the snowy region in Prince William Sound can help meet conservation goals for the species, but these areas should be evaluated using longer-term climate models. Climate forecasts beyond the 100-year span of those currently used are needed in order to plan conservation measures for long-lived tree species.

At a more local landscape scale, yellow-cedar appears healthy on well-drained soils, where it mixes with other tree species, even in areas of little snow accumulation, where adjacent dead cedar forests exist on wet soils. It is on these productive sites that yellow-cedar roots more deeply and reaches its greatest stature but not its greatest competitive status (Harris 1990). Western hemlock and Sitka spruce (*Picea sitchensis* [Bong.] Carrière) can outcompete yellow-cedar through greater rates of reproduction and faster growth, but active forest management can favor yellow-cedar. These productive sites have received most of the timber harvesting in the region; therefore, this is the primary active-management space that is available to achieve conservation goals for yellow-cedar. Favoring yellow-cedar through planting and thinning will effectively expand yellow-cedar's realized niche. More silvicultural information is needed on the techniques of managing yellow-cedar in young-growth forests to ensure the long-term maintenance of the species.

The migration zone: Dispersal of yellow-cedar to new habitat areas with suitable climates. When favorable climate develops beyond its existing range, yellow-cedar may be particularly slow to migrate because of its low reproductive capacity (Harris 1990). The previously mentioned genetic study is designed to test the Holocene migration of yellow-cedar, which we suspect is slow and still proceeding toward the northeast. Yellow-cedar is absent from much of the widespread forested wetland in these areas, even though the conditions appear to be favorable for yellow-cedar and may have been so for thousands of years. Yellow-cedar may benefit from some assistance in migration to speed the colonization of new habitats as the climate warms.

Assisted (or *facilitated*) *migration* is the deliberate movement by humans of genotypes and species into areas in which the projected climate is believed to be associated with high probabilities of persistence. These activities can be controversial, because widespread movements of species can be interpreted as fostering the introduction of invasive species that could bring unanticipated consequences. Assisted migration may be required for species with narrow resource requirements or poor dispersal ability (Warren et al. 2001), such as yellow-cedar. As a cautious step, we conducted a trial planting of yellow-cedar near Yakutat, Alaska, (an area of discontinuous occurrence for yellow-cedar but still within its range limits; Hennon and Trummer 2001) to test the survival and growth of yellow-cedar where it did not previously grow. The first-year survival rate was over 90%, which suggests that the targeted expansion of yellow-cedar is possible.

Conclusions

We used the case of yellow-cedar decline to illustrate how climate can interact with other factors to initiate widespread tree mortality. In this article, we documented the approaches that we used to determine the etiology of a classic forest decline, to expose the role of climate, and to develop a dynamic conservation strategy. Lessons from those experiences may be of use to scientists and forest managers challenged with other issues related to the interaction of climate and forest health.

A combination of deductive and inductive methods is useful to resolve the etiology of forest declines and other problems with complex causes. There is probably no substitute for pathologists and entomologists investigating the symptoms of dying trees and the potential involvement of biotic agents before interpretations are made on the causes of those deaths. Our example revealed a direct influence of climate on a tree species decline, but climate can also favor insects and tree pathogens, which may initiate widespread injury to forests. The temporal and spatial patterns of tree death offer invaluable clues for building and evaluating hypotheses, but mechanistic physiological studies are needed in order to provide a credible explanation of climate effects where they might exist. Climate is not the only factor that needs to be examined, because it will not act alone to cause tree death. Site factors will likely interact with climate to affect tree species' survival, especially those key factors that define a species' niche. It is perhaps not surprising that we found that the ecological-niche factors that contribute to the distribution and competitive status of yellow-cedar also operate as risk factors for its decline. Therefore, climate models are useful as a broad-scale tool, but they need to be supplemented with information on species vulnerabilities and niches in order to develop specific adaptive strategies.

Conservation and restoration strategies must acknowledge the dynamic nature of climate, and the locations of their application must therefore be chosen carefully to account for future change. Active forest-management strategies can take several forms, such as the movement of species and specific genetic forms through assisted migration and the favoring of conditions for a species through niche expansion. Species of great cultural, economic, or ecological value, such as yellow-cedar, attract interest from research institutions in the evaluation of the impacts of altered climate and other threats. The potential applications of research are more likely to be put into action as policymakers and forest managers become willing to use resources to conserve or manage valuable species. The lessons learned from initial work on a few high-value species could inform efforts to monitor and manage the influences of a changing climate on a wide variety of forest species.

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