

Emerging climate-driven disturbance processes: widespread mortality associated with snow-to-rain transitions across 10° of latitude and half the range of a climate-threatened conifer

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Abstract

Climate change is causing rapid changes to forest disturbance regimes worldwide. While the consequences of climate change for existing disturbance processes, like fires, are relatively well studied, emerging drivers of disturbance such as snow loss and subsequent mortality are much less documented. As the climate warms, a transition from winter snow to rain in high latitudes will cause significant changes in environmental conditions such as soil temperatures, historically buffered by snow cover. The Pacific coast of North America is an excellent test case, as mean winter temperatures are currently at the snow–rain threshold and have been warming for approximately 100 years post-Little Ice Age. Increased mortality in a widespread tree species in the region has been linked to warmer winters and snow loss. Here, we present the first high-resolution range map of this climate-sensitive species, *Callitropsis nootkatensis* (yellow-cedar), and document the magnitude and location of observed mortality across Canada and the United States. Snow cover loss related mortality spans approximately 10° latitude (half the native range of the species) and 7% of the overall species range and appears linked to this snow–rain transition across its range. Mortality is commonly >70% of basal area in affected areas, and more common where mean winter temperatures is at or above the snow–rain threshold (>0 °C mean winter temperature). Approximately 50% of areas with a currently suitable climate for the species (<−2 °C) are expected to warm beyond that threshold by the late 21st century. Regardless of climate change scenario, little of the range which is expected to remain suitable in the future (e.g., a climatic refugia) is in currently protected landscapes (<1–9%). These results are the first documentation of this type of emerging climate disturbance and highlight the difficulties of anticipating novel disturbance processes when planning for conservation and management.

Keywords: Alaska yellow-cedar, biogeography, *Callitropsis nootkatensis*, climate change, climate refugia, emergent disturbance, forest disturbance, precipitation, protected area, snow

Received 3 July 2016; revised version received 27 October 2016 and accepted 29 October 2016

Introduction

Disturbances such as fire, wind, and insect outbreaks are common processes in the world's forests and exert a significant influence on broad-scale carbon balance, habitat, and ecosystem functions (Pickett & White, 1985; Running, 2008; Allen *et al.*, 2010; van Lierop *et al.*, 2015).

Climate change is already affecting forest dynamics and disturbance regimes, as timing, intensity, and duration of events are already shifting (Dale *et al.*, 2001). In the conterminous United States, broad-scale forest disturbances are currently dominated by 'decline-type mortality events' (also referred to as forest dieback), which are affecting approximately 5–10 times as much area as fire; annual percentage of areas in decline, which include insect mortality, have risen 21-fold from 1985 to 2012 (Cohen *et al.*, 2016). These decline events are often

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triggered by the crossing of environmental thresholds which change scale-dependent controls on biotic processes (e.g., mountain pine beetles; Raffa *et al.*, 2008) or which push species beyond physiological tolerance limits (e.g., sudden aspen decline; Anderegg *et al.*, 2012). These may represent 'emerging' disturbance processes, previously infrequent or unknown processes resulting from novel climatic conditions, or unexpected disturbance interactions (Paine *et al.*, 1998; Buma, 2015). These emergent processes are especially difficult to anticipate, but extraordinarily important to understanding forest change in future no-analog climate conditions (Seidl *et al.*, 2011).

One type of emergent disturbance processes that is rarely considered in projections of forest change is mortality associated with the loss of freezing temperatures and changing snow extent/cover. The loss of continuous days of subzero temperatures has important implications for thermal conditions in forests, and has, paradoxically, resulted in frost damage for many plant species, especially on new vegetative growth in early spring (Gu *et al.*, 2008; Inouye, 2008). Attempts to predict this damage have typically focused on the physiology of sensitive bud tissues (e.g., Hänninen, 2006; Rigby & Porporato, 2008); as such, damage can reduce or eliminate annual growth. Although frost damage can kill young seedlings, mature trees are generally expected to survive these events (Augspurger, 2013).

Climate warming is also causing a general reduction of snow cover in most locations, with the boundaries (margins) of areas that currently receive reliable winter snow seeing the largest change (Adam *et al.*, 2009). The transition from a consistent winter snowpack to a winter where the ground is generally snow-free has important implications for species dependent on the subnivium (Pauli *et al.*, 2013). Snow is an effective thermal insulator for soils (Decker *et al.*, 2003), and the loss of snow exposes tree roots to potentially lethal temperatures during freezing events (Groffman *et al.*, 2001; Schaberg *et al.*, 2008), soil nutrient losses (Tierney *et al.*, 2001; Matzner & Borken, 2008), soil moisture decreases (Hardy *et al.*, 2001), and ultimately tree death (Hennon *et al.*, 2012).

The emergence of widespread mortality resulting from a loss of snow cover has not been well studied; research has focused more on frost damage to plant organs (e.g., bud tissue). However, given the rapid loss of snow cover expected over the next century, it is important to examine the potential importance of this phenomenon (Pauli *et al.*, 2013). The Pacific coast of North America is ideally suited for studying such a shift, as a broad stretch of area spanning several degrees of latitude is currently at that freezing threshold; thus, only minor warming is required on average to switch winter

precipitation from snow to rain (Fig. 1). Natural climatic variability, generally associated with the Pacific Decadal Oscillation (PDO) is already causing periodic snow-free winters. Human presence relatively low and tree species composition is very similar across approximately 20° of latitude, with wet forests characterized by western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*). As a result, response to the snow-to-rain shift can be monitored without confounding effects of different forest types or human intervention.

In those forests, substantial mortality linked to a transition from reliably snowy winters to generally rain-dominated winters has been ongoing for several decades (Hennon *et al.*, 2012). Yellow-cedar (*Callitropsis nootkatensis*), a culturally, economically, and ecologically significant tree which extends across ~20° of latitude, has experienced increased mortality across broad swathes of its range for about a century associated with a loss of snow cover and subsequent root freezing in uninsulated soils during cold weather events (Schaberg *et al.*, 2008; Stan *et al.*, 2011; Hennon *et al.*, 2012). This mechanism has been well described using both experimental- (e.g., Schaberg *et al.*, 2008) and observation-based studies (e.g., D'Amore & Hennon, 2006); fine root mortality and subsequent necrosis result when soil temperatures (upper ~5 cm) descend below -5 °C (Schaberg *et al.*, 2008). Total tree mortality can be rapid, within a single year, or more typically cumulative over successive root-freezing events (Hennon *et al.*, 2016). Differences in rates are usually attributed to varying microsite conditions which influence rooting depth (Hennon *et al.*, 2016). This lack of snow cover related mortality has been noted in both Alaska and British Columbia, generally approaching 70% of yellow-cedar basal area in affected areas (Hennon *et al.*, 2016). Yellow-cedar often dominates intermediate productivity sites with moderate drainage (>75% of basal area) and is a minor to major component in other portions of its range as well. The only succession-focused study suggests a long-term reduction of yellow-cedar in the landscape and subsequent replacement by other regionally common tree species already present in these locations (Oakes *et al.*, 2014). This emerging disturbance and mortality process, known as 'yellow-cedar decline', is causing a general community simplification. Because the mortality is extensive and tied to climate warming, which is expected to be rapid at high latitudes, there is a concern that much of the currently healthy yellow-cedar forests may die-off rapidly in the future (Krapek & Buma, 2015; Oakes *et al.*, 2015). As a result, yellow-cedar is under consideration for endangered species listing in the United States. Substantial amounts of the landscape are under some form of protection from harvest in the form of wilderness areas or nature reserves.

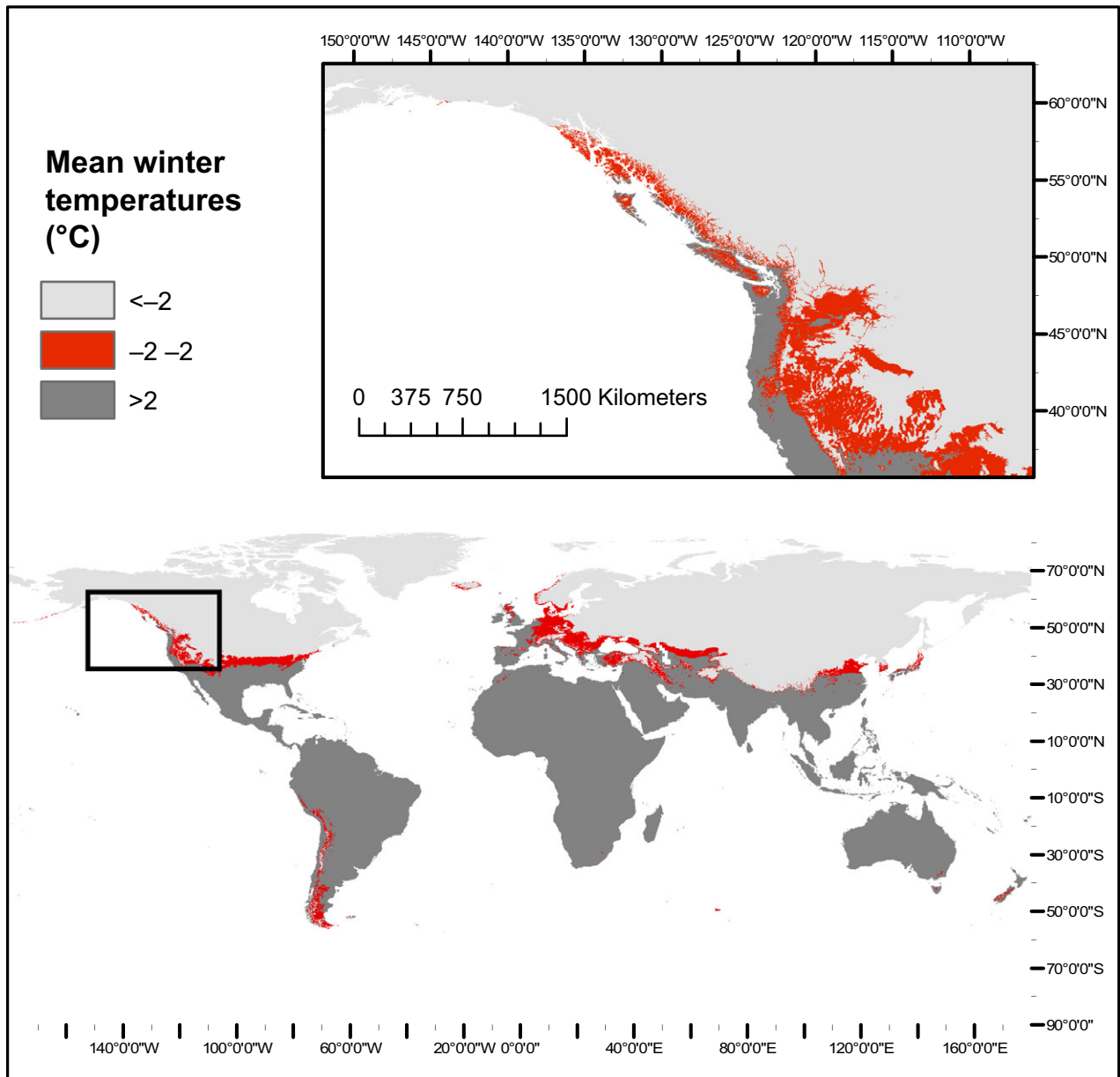


Fig. 1 Areas where mean winter temperatures are relatively close to the snow–rain threshold, here defined as -2 to 2 °C. The Pacific coast of North America (inset) offers a long latitudinal gradient at that threshold with consistent species composition ideally suited to studying the effects of this snow-to-rain precipitation shift. Data from Hijmans *et al.* (2005).

A key challenge of any conservation efforts via protected areas is the conflict between shifting climate and static (in terms of location) reserve areas (Hannah *et al.*, 2007). Understanding how much protected area will shift from being climatically suitable to unsuitable is extremely important in anticipating future conservation or protection needs.

Yellow-cedar decline represents a specific example of a potentially widespread phenomenon. The ecological competitive strategy of shallow rooting and active

metabolism in spring (D'Amore *et al.*, 2009) is not uncommon in plant communities. Species which express this growth pattern are generally taking advantage of early spring sources of available nutrients (often nitrogen); it is likely that many plant communities in temperate- and high-latitude systems contain species utilizing this strategy which evolved under historic climate regimes. Expected losses of winter freezing conditions (globally) is most pronounced along the North Pacific coast (Meehl *et al.*, 2004), making this region a

useful area to explore the implications of this emerging climate shift. This loss of snow will eventually occur throughout high-latitude regions; thus, this phenomenon is potentially the beginning of a more widespread pattern. This is the first study to document the range of snow cover loss induced forest mortality across 10° of latitude and two countries.

Questions

- 1 What is the extent of mortality both by latitude and elevation and how does that relate to the species range?
- 2 Are broad-scale mortality patterns consistent with the mechanistic understanding of the decline developed through experiments and plot-level research?
- 3 How will conditions associated with mortality shift geographically in the future and to what extent will these conditions impact currently protected areas?

Materials and methods

We created a GIS layer for mortality of yellow-cedar from aerial forest health surveys in British Columbia (2006–2014) and in Alaska (1990–2014; Hennon *et al.*, 2016). Mapped patches of yellow-cedar with elevated dead individuals (snags) represent cumulative mortality and include old and recent standing dead and dying trees, all of which are visible from the air. In British Columbia, a category of ‘trace mortality’ or scattered individual dead or dying yellow-cedar trees was present; it was not used because that category did not exist in the Alaska data, the cause of death was unclear, and to remain conservative in our estimates. Higher resolution layers of yellow-cedar decline mapped from aerial photographs were available for several specific areas in Alaska as validation data and showed strong geographic alignment with the aerial survey mapping layer (Hennon & Wittwer, 2013). Surveyors have searched for but not confirmed mortality further south in Canada (49–51°N) and further north in Alaska (>58°N); mortality in the contiguous United States has not been specifically observed.

Yellow-cedar occurrence data were combined from three sources. For the Alaskan portion, the range was constructed using the Ellenwood *et al.* (2015) habitat modeling methodology. Briefly, this approach utilizes a variety of geospatial data, including soil (STATSGO2), land cover (NCLD), forest inventory data (FIA), and climate to create a statistical model which is then translated to a geospatial map coverage; see Krist *et al.* (2014) and Ellenwood *et al.* (2015) for more information. While originally constructed at 30 m, to expand the Ellenwood model across the entire range of yellow-cedar, it was down-scaled to 240 m to match data availability. Isolated populations beyond the modeled area above in Prince William Sound (Hennon & Trummer, 2001), Glacier Bay National Park (Oakes *et al.*, 2015), and Haines and Icy Bay (Hennon *et al.*, 2016) were added to the final map for completeness; these areas make up <0.1% of the total range area. Accuracy of the Ellenwood *et al.*

(2015) model is considered very strong for both percent agreement between statistical model (99.8%) and the final map model (99%). This product was utilized for the Alaskan portion of the range.

This approach corresponds with the British Columbia (BC) Vegetation Resource Inventory (VRI) programme maps land cover, including the occurrence of the six most abundant tree species for every treed forest cover polygon on the landscape using a combination of midscale, calibrated air photo interpretation, biophysical data, and subsequent ground sampling. The border between the Alaskan and BC layers was visually interpreted for correspondence. The VRI data are available for the majority of the expected range in BC, but private lands and inholdings were not always included in the range map (depending on data availability). This produces a slight underestimation of overall range, but this is limited to a small latitudinal range and not all of these areas are suitable habitat, as most of the gaps extend above tree line. We report the entirety of the missing area for consistency (Table S1).

For the southern portion of the study area (Washington, Oregon, and California; WaOrCa hereafter), the US Forest Service (USFS) utilized a different mapping method corresponding to yellow-cedar habitat suitability rather than presence, which overestimates actual yellow-cedar occurrence (Ohmann & Gregory, 2002). To align these data with the Alaskan-BC layer, we matched statistical accuracy between the layers. First, we assessed the accuracy of the Canadian map (presence only) with a set of independent data points not used in model construction ($n = 1349$). We calculated the number of points with yellow-cedar that were modeled as containing the species, with a 1 km spatial tolerance (buffer) to accommodate geolocal error, similar to validation methods used by the USFS aerial survey (Johnson & Ross, 2008). Any points within 1 km of each other were combined into a single point. Accuracy was 74.10% (1000/1349). We progressively removed low suitability points from the WaOrCa starting at the lowest suitability until a similar accuracy (72.95%) was achieved using another independent dataset (presence-only; $n = 207$) for the WaOrCa area. The end result is a seamless map with similar accuracy across all borders, from ~61°N in southcentral Alaska to 42°N in northern California. Known outlying populations in eastern Oregon, Prince William Sound Alaska, and northern California were added manually for completeness; these populations are small and do not influence the results (see Hennon *et al.*, 2016 for details on various sources). All range data were developed at 240 m spatial resolution.

Winter/snow climate data

Climate information for current and future conditions is from WorldClim (Hijmans *et al.*, 2005). WorldClim was chosen because it presents a consistent methodology for the entire study area (~20° of latitude) and a relatively fine resolution (~1 km). To remain conservative, the data were down-scaled to the resolution of the final range map via nearest neighbor interpolation. We used the mean winter temperature data

(defined as the mean temperature during the coldest 3 months of the year, which varies across the gradient) as a measure for snow vs. rain. For example, an area which switches from averaging below freezing to above freezing is assumed to also switch from primarily snow to primarily rain-driven precipitation (Shanley *et al.*, 2015). For future climates, we utilized the projections derived from Hadley GEM2-ES model for both the RCP2.6 and RCP8.5 scenarios. These climate futures were chosen to bracket the range of potential future climates. The Hadley model showed consistently high correlations with observed data vs. five different GCM's evaluated by the Scenarios Network for Arctic Planning (SNAP 2009) when considering variables we were concerned with – monthly mean temperature, interannual temperature variability, and temperature trends, as evaluated over all stations in the coastal forest.

Protected area maps

To estimate the extent to which yellow-cedar populations will be protected from human activities and adverse climates in the future, we assessed protected status alongside climatic suitability. Protected areas were taken from the World Database on Protected Areas (IUCN & UNEP-WCMC 2016), a joint effort between the United Nations Environmental Programme and the International Union for the Conservation of Nature. The newly founded Great Bear Rainforest (GBR)-protected area in British Columbia, established in January 2016, is not yet fully included in the IUCN database and was added using maps provided directly by The Sierra Club and BC Ministry of Forests. Protected inholdings administered by The Nature Conservancy as part of the GBR were also included. Special forest management areas, which generally allow some types of intense management, were not classified as protected for this analysis.

Statistical tests

Correlations between topography, latitude, and presence and mortality data were assessed via linear regressions. Because both the mortality and range data are spatially autocorrelated, we first randomly subsampled 1000 locations from across the range. This reduces statistical power but similarly reduces spatial autocorrelation in the tested data. Subsamples met assumptions for normality and heteroscedasticity of errors required for linear regressions. To isolate the role of mean winter temperature from the topographic variables (elevation, slope, and aspect), random forests (Breiman, 2001) were used. Random forest models are appropriate for interacting variables where interaction terms can change across the range of the data. A total of 500 trees (sampled with replacement) were created, and the partial dependency of mortality as a function of temperature was then quantified. This approach controls for the covariation of other variables across the range of observed temperatures by estimating the marginal effect of a single variable while holding the other variables at their mean value; in this case, the effect is the probability of a location characterized as declining. All data were projected in Albers Equal Area using ArcGIS; all statistics were completed in R (R Development Core Team, 2015).

Results

The current natural range of yellow-cedar spans 20° latitude and covers approximately 56 000 km² (Table 1, Fig. 2); it is primarily constrained to a narrow strip along the Pacific coast. There are four geographically isolated population areas in eastern Oregon (Frenkel, 1974), southeastern British Columbia (Perry, 1954), Icy Bay (Hennon *et al.*, 2016), and Prince William Sound at the northwestern range edge (Hennon & Trummer, 2001). The elevation of the range increases as latitude decreases, from sea level in the north to tree line in the south ($P < 0.001$, $r^2 = 0.4$, Fig. 3a). Topographic slope of yellow-cedar stands marginally increases to the south ($P < 0.001$, $r^2 = 0.04$, Fig. 3b), while aspect does not significantly change ($P > 0.05$, Fig. 3c). Mean winter temperatures show no trend across latitude throughout the range ($P > 0.05$, Fig. 3d).

Of the area within yellow-cedar's range, about 4000 km² are experiencing induced mortality (Table 1, Fig. 2), approximately 7% of yellow-cedar's range. A total of 52 337 km² are currently presumed healthy as they lack the intensive mortality detected in aerial surveys. The mortality is concentrated in the northern 10° latitude where largest populations occur, though not in the small and scattered populations at the extreme northern edge. The percentage of yellow-cedar forest affected is >17% in some areas (56–57°N; Table S1). Mean elevation in mortality-affected areas steadily increases from north to south ($P < 0.001$, $r^2 = 0.34$, Fig. 3a) – mortality is more common at lower elevations in the north and higher elevations in the south, following the hypothesized rain–snow line. In terms of slope and aspect, mean slope in mortality areas marginally increases further to the south, though the trend was significant ($P < 0.001$, $r^2 = 0.10$), and mortality was not associated with any particular aspect ($P > 0.05$). Across the range of observed mortality, decline was more likely in areas near the freezing threshold of 0 °C mean winter temperature, and found in slightly warmer areas in the south though with substantial variation ($P < 0.001$, $r^2 = 0.06$). The –2 °C threshold did capture

Table 1 Area of yellow-cedar presence and climate-induced mortality by latitude. For individual latitude, bands and area not included in Canadian range model (which does not affect mortality estimates), see Table S1

| Latitude band | Healthy area (km ²) | Mortality area (km ²), % | Total area (km ²) |
|---------------|---------------------------------|--------------------------------------|-------------------------------|
| 60–62 | 43 | 0.0/0 | 43 |
| 55–60 | 19 792 | 2779/12 | 22 571 |
| 50–55 | 24 974 | 1214/5 | 26 187 |
| 45–50 | 7427 | 0.0/0 | 7427 |
| 41–45 | 101 | 0.0/0 | 101 |

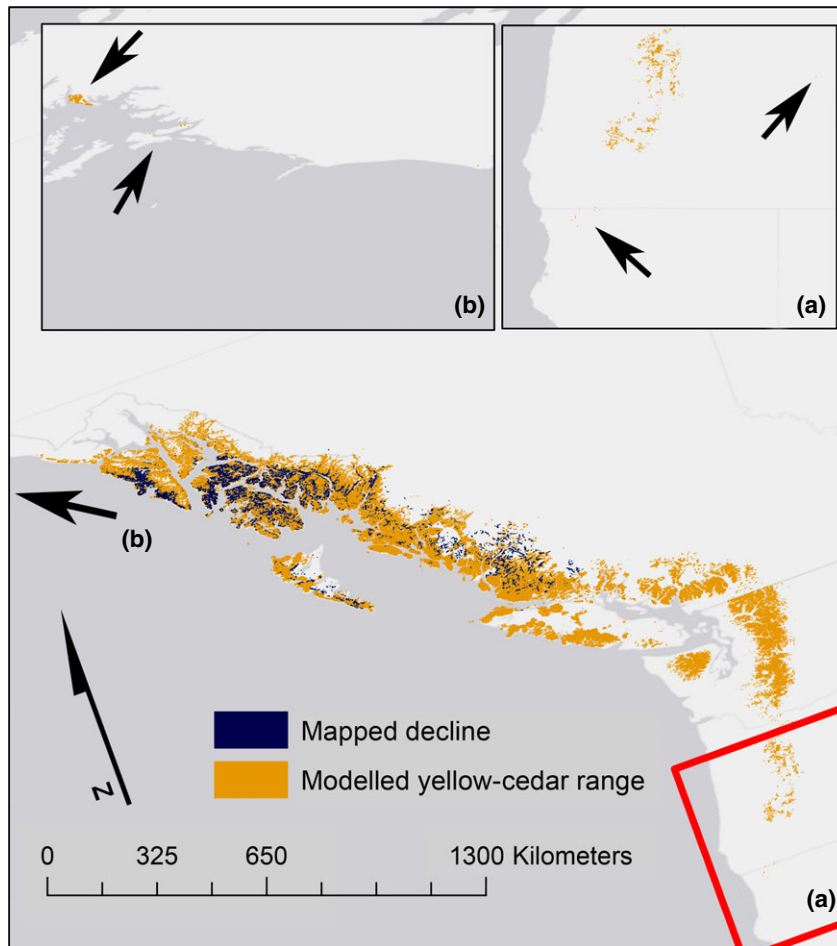


Fig. 2 New range layer of yellow-cedar and observed mortality. Insets show detail at extreme range edge. (a) Northern California and southern/eastern Oregon (red box). (b) Prince William Sound and Icy Bay. Inset arrows show small, disjunct populations.

the majority of mortality across the range of the species (Fig. 3d). The random forest algorithm was successful in classifying mortality (mean error 18%, 500 trees). Mortality status (declining or healthy) was sensitive to temperature from approximately -4 to $+2$ °C, with the highest chance of mortality from -2 to 2 °C (Fig. S1).

Future projections and protected status

By 2070, substantial areas of yellow-cedar forests are expected to shift to above-freezing mean winter temperatures (Fig. 4), suggesting increasing vulnerability to mortality. Estimates of area vary depending on the threshold chosen (Table 2); using a mean winter temperature of 0 °C as an indicator of vulnerability result in 30–45% of currently healthy area shifting to vulnerable by 2070. If a lower threshold of -2 °C is chosen, as suggested by the observed pattern (Fig. 3d), the estimated potential extent of mortality expands to 45–50% of the currently healthy populations (Table 3).

Not all areas above the winter snow threshold are experiencing mortality, although die-off in these areas may continue in the future. For areas that will likely cross the snow–rain threshold by 2070, modifying the total area (Table 3) by the proportion of the landscape already above freezing and also dying (3.9–15.8%, depending on latitude; Table 2) results in a potential future threat to approximately 3.5–8% of currently ‘climatically safe’ areas. This represents a lower end estimate of potential future mortality, as mortality is still ongoing in currently vulnerable areas. Of the areas expected to remain below that mortality threshold, relatively little is in protected status, ranging from 2% to 9% using the 0 °C threshold and <1% to 3% using the -2 °C threshold (Table 3). Projections broken down by latitude are available in Table S1.

Discussion

The range of yellow-cedar is broad north to south, but limited east–west to a narrow strip of coastal forest and

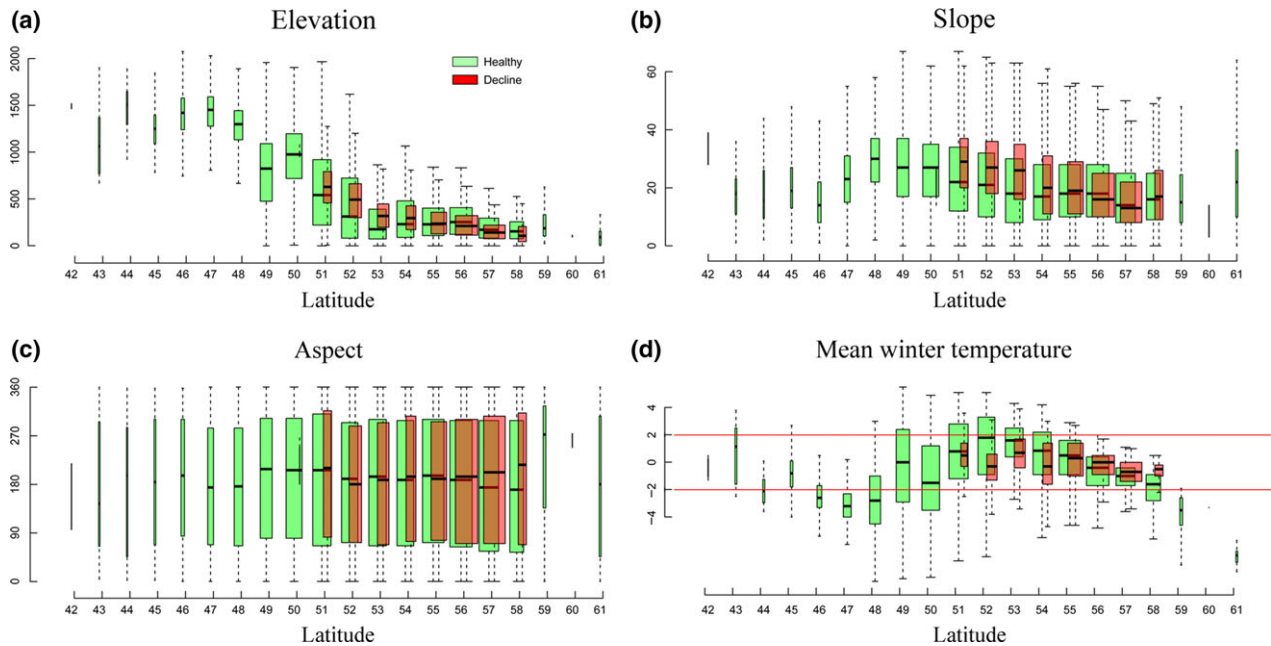


Fig. 3 Distribution of yellow-cedar and observed mortality as a function of latitude and relative to (a) elevation (m), (b) slope (degrees), (c) aspect (degrees), and (d) mean winter temperature ($^{\circ}\text{C}$, coldest quarter of year). Both yellow-cedar and yellow-cedar decline occurrence increase in elevation at lower latitudes. Decline is generally limited to temperatures between $+2$ and -2 $^{\circ}\text{C}$ (horizontal lines). The healthy populations are generally in colder regions in both the north and south part of the range. Note box plots are shown for clarity, and all regressions were plotted on individual data points. Width of plots reflects relative area within healthy or declining populations individually, not comparatively.

a narrow temperature band, generally around 0 $^{\circ}\text{C}$ in the winter. To the south, yellow-cedar increases in elevation, to follow that climate zone. Mortality resulting from recent warming and subsequent loss of snow cover is currently extensive, affecting populations across approximately $\frac{1}{2}$ of the range by latitude and 7% of the total area (Fig. 2). Mortality is generally concentrated in portions of the range with current temperatures near zero in winter, as expected given the mechanisms of this emerging disturbance process. There are healthy populations in areas well above the winter freezing point (though limited in spatial extent) and in areas well below that threshold (Fig. 3).

In warmer areas, it is likely that while there is little snow coverage, there is also little chance of frequent cold, soil freezing conditions. For example, a large area approximately 50°N on the west side of Vancouver Island has no documented mortality despite temperatures >0 during the winter. This is likely due to the infrequency of prolonged cold snaps, as it is protected from the cold interior continental air mass by large distances and multiple mountain ranges. While a simultaneous reduction in cold snaps in spring could reduce risk of mortality even in the absence of snow, no decline in the probability of freezing events has been noted through the 20th century despite the generally

warming winters and lesser snowpack further north (Beier *et al.*, 2008). Ultimately, projections for the future indicate that areas exposed to potentially decline-triggering temperatures will expand greatly, to approximately 50% of the entire range by 2070 (Table 3).

Several surveys of mapped decline areas across the range show high rates of mortality in terms of basal area: 66–69% mortality ($n = 50$; Hennon *et al.*, 1990); two areas showing 71–74% and 75–79% mortality ($n = 47$ and $n = 29$, respectively; D'Amore & Hennon, 2006); and another area at 82–85% mortality ($n = 30$; Oakes *et al.*, 2014). When nondecline and mixed forest areas are included in broader surveys, mortality is still elevated. In two locations, Hennon *et al.* (1990) report basal area mortality in mixed decline/healthy areas as 54% ($n = 80$) and 34% ($n = 64$). In British Columbia, Stan *et al.* (2011) found 37% basal area mortality in yellow-cedar across four sites ($n = 12$). These values can be compared to live areas with typical dead basal area proportions at approximately 13% ($n = 18$; Oakes *et al.*, 2014).

Nevertheless, not all yellow-cedar exposed to warmer temperatures die as microsite variation can provide some protection despite a lack of snow. While yellow-cedar is not generally considered competitive with faster growing species in well-drained soils, it does occur in these areas where yellow-cedar roots

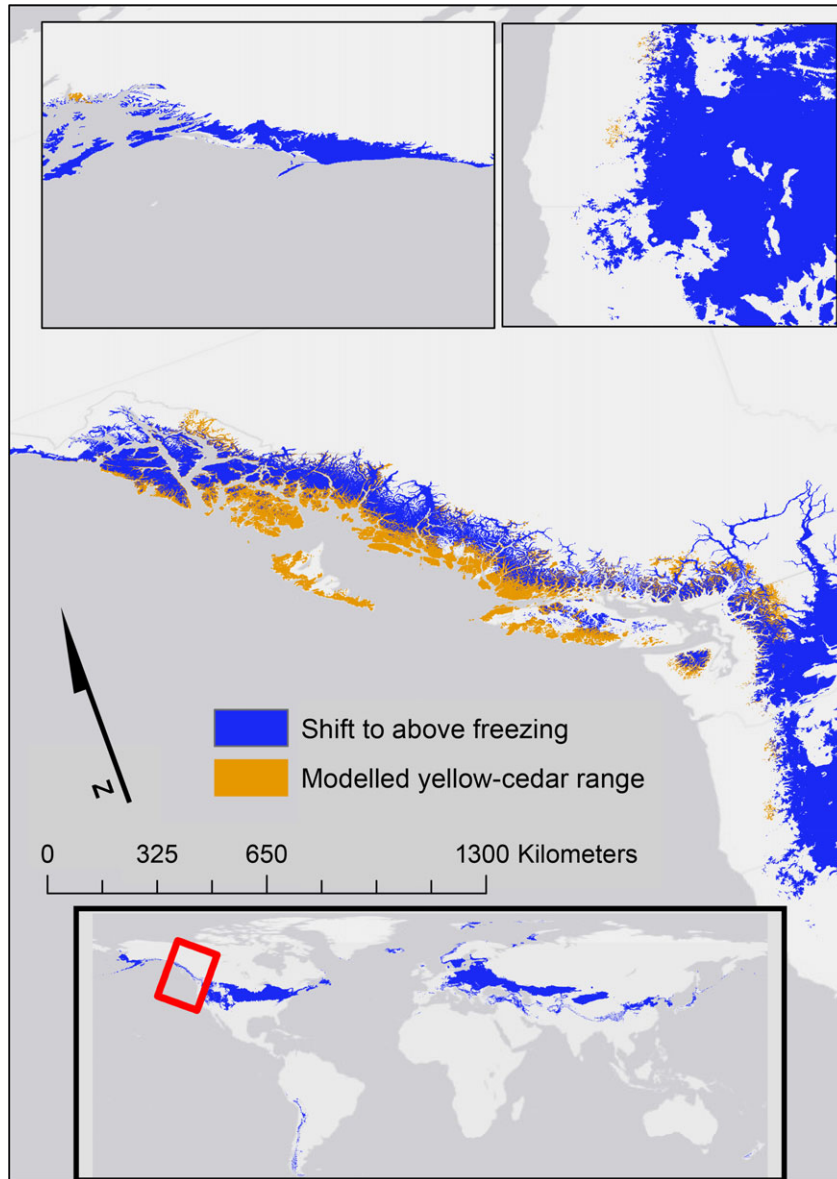


Fig. 4 Rangewide area expected to shift to above freezing (mean winter temperature) under the Hadley ES RCP8.5 scenario by 2070 (extent and insets identical to Fig. 1). Globally, significant area is expected to shift, especially in eastern Europe, Scandinavia, Chile, and New Zealand.

relatively deeply and generally lower amounts of mortality are observed (Hennon *et al.*, 2016). In addition, mass mortality does not occur every year (Stan *et al.*, 2011), as it requires the confluence of low snow and late-season cold events and can require multiple injury events to different areas of the rooting system to result in complete tree death. Short-term repeat USFS Forest Inventory and Analysis (FIA) measurements recently found little additional mortality in the mid-2000s (Buma & Barrett, 2015), although the time period of observation was short and the climate generally cooler, with significant snowfall. Currently, the proportion of

the landscape both above the freezing threshold and experiencing mass decline range from 3.9% to 15.8% (Table 2); in other words, not all areas experiencing the adverse climatic conditions are also experiencing mass mortality due to mitigating factors driven by topography and drainage (rooting depth) or a lack of concurrent cold snaps. This intersection of multiple drivers creates the observed heterogeneity at fine scales – patterns of mortality arise from the confluence of topographically controlled drainage patterns, climatically controlled low snow conditions, and stochastic yearly weather (cold snaps).

Table 2 Area-weighted proportion of yellow-cedar mortality by temperature threshold (mean temperature of the three coldest months) and latitude band

| Latitude | % Area below 0 °C | % Area above 0 °C | % Area below -2 °C | % Area above -2 °C |
|-----------|-------------------|-------------------|--------------------|--------------------|
| 60–62 | 0* | 0* | 0* | 0* |
| 55–60 | 11.1 | 15.8 | 6.4 | 14.1 |
| 50–55 | 6.9 | 3.9 | 4.3 | 5.0 |
| <50 | NA | NA | NA | NA |
| Rangewide | 7.7 | 6.7 | 3.6 | 8.2 |

Percentages refer to percent of total range within the latitude band (including healthy areas), and thus do not sum to 100%. For individual latitudinal bands, weights are relative to area within those bands. For rangewide proportions, weights are relative to the entire rangewide area of the species.

*No mortality observed >60° latitude.

Table 3 Temperature thresholds (mean temperature of three coldest months) and expected extent of additional vulnerable landscapes in 2050 and 2070 by climate scenario and protected status

| | RCP2.6* | | RCP8.5* | |
|------------------------------------|---------------------------|---------------------------|---------------------------|---------------------------|
| | 2050, km ² (%) | 2070, km ² (%) | 2050, km ² (%) | 2070, km ² (%) |
| Above 0 °C | 15 284 (29) | 15 815 (30) | 20 150 (39) | 23 705 (45) |
| Above -2 °C | 23 135 (44) | 23 291 (45) | 24 942 (48) | 26 036 (50) |
| Below 0 °C (protected areas only) | 4812 (9) | 4526 (9) | 2482 (5) | 1093 (2) |
| Below -2 °C (protected areas only) | 1376 (3) | 1346 (3) | 632 (1) | 168 (<1) |

Percentages express new area of the range above each threshold, not cumulative area above each threshold. For areas on a per latitude basis and cumulative area above the thresholds, see Table S1.

*Percentage values are relative to currently healthy landscapes only (excluding current mortality).

While drainage is essentially a static, unchanging driver of susceptibility, the confluence of low snow and late-season cold is variable. Given the punctuated nature of the mortality triggering events (Stan *et al.*, 2011; Hennon *et al.*, 2016), additional mortality will continue to occur in those areas already above the winter snow threshold, especially if they are susceptible due to shallow rooting in poorly drained areas. As a result, the proportion dead in currently vulnerable areas will likely rise above what has been observed (3.9–15.8% depending on latitude, Table 2). This will increase expectations of future mortality in currently suitable habitat as those areas being to experience lower snow accumulations. Ultimately, approximately 50% of currently cold habitat is expected to be exposed to decline-triggering conditions, and cumulative mortality in the future will, as now, depend on the intersection of fine-scale susceptibility drivers, climate, and year-to-year temperature fluctuations.

This disturbance process has broader ecosystem implications as well. Fine root mortality, even if not fatal to the tree, can result in nutrient loss from systems as uptake is limited in early season when highly mobile nutrients are present in the soil (Tierney *et al.*, 2001). Nitrogen limitation is a common trait of

temperate forests, and loss of nitrogen can reduce ecosystem productivity (Vitousek *et al.*, 1979; Krana-better *et al.*, 2016). Many disturbance processes result in community and successional shifts that include nitrogen fixing species – in the case of the North Pacific coastal forests, *Alnus* species are common early postdisturbance pioneers and add significant amounts of nitrogen to recovering forests (Perakis *et al.*, 2015). However, regeneration postcedar mortality is limited to late successional species (Oakes *et al.*, 2014), likely due to the minimal soil disturbance and lack of disruption to the understory/seedling community. It is notable that other disturbances which similarly do not disrupt the soil and encourage N-fixer activity have not resulted in substantial nitrogen loss (Rhoades *et al.*, 2013). This has been attributed to a combination of recovering vegetation uptake and a patchy disturbance process. However, these results come from warmer climates with more rapid decomposition and less nutrient sequestration in living/dead biomass. In colder forests, such as those that would be exposed to these types of emerging disturbance processes, nitrate losses due to limited uptake (Tierney *et al.*, 2001) coupled with increased nitrogen sequestration in both living and dead biomass may have long-term

implications for ecosystem productivity (McLauchlan *et al.*, 2014).

This emerging disturbance may be a leading indicator of change in other forest and mountain systems. The North Pacific coast is the area expected to experience the largest change in freezing conditions over the next several decades (Meehl *et al.*, 2004) but not the only area worldwide, and broad swaths of coastal and continental landscapes will likely experience low/no snow conditions in the future. At the same time, stochastic variation in weather will likely continue to supply freezing conditions in late winter/spring, when soils have historically been insulated by snow, at least in high-latitude or high-elevation portions of the many species ranges (Beier *et al.*, 2008). Climate-driven disturbance processes generally occur as a function of extreme events, rather than following the mean, causing significant, broad-scale, and potentially permanent changes in relatively short, punctuated intervals (known as the 'ratchet of events'; Jackson *et al.*, 2009). This rapidly changing snow environment has implications for a variety of processes, such as nutrient cycling (Pauli *et al.*, 2013) and forest-related functioning (e.g., habitat, carbon sequestration; Buma & Barrett, 2015). The potential for new disturbance processes to emerge is a significant challenge for ecosystem planning, management, and modeling. For areas anticipating a switch from snow-to-rain dominance, one strategy for anticipating communities and areas of vulnerability will be to examine species with a similar competitive strategy (shallow rooting and metabolic activity) or a tendency toward wet habitats which require shallow rooting.

One option for adapting to climate change is habitat protection and conservation (DellaSala, 2011). The presence of climate refugia (i.e., regions where climate will remain suitable) are important considerations when predicting the viability of a species. Only a relatively small percentage of the currently healthy forests are both protected now and expected to remain suitable (in terms of winter temperatures) in the future. A fundamental challenge to conservation in the context of a shifting climate is that protected areas are generally static, requiring conservation and management planning for migrating species outside of protected areas, establishing protected areas in anticipation of range shifts, and adaptive management options (Hannah *et al.*, 2002; Hobbs *et al.*, 2009). Static boundaries of protected areas represent a fundamental challenge to conservation in a changing climate, and areas once set aside for preserving species may be insufficient (Heller & Zavaleta, 2009). Future conservation strategies may require incorporating lands outside protected areas (Kareiva, 2014) and implementing new active management practices, like planting, assisted migration (McLachlan *et al.*,

2007), expanding reserves (Beier & Brost, 2010), and other adaptive options (Hannah *et al.*, 2002; Buma, 2013). Oakes *et al.* (2015) found broad acceptance for a portfolio of practices across land designations for yellow-cedar including, for example, experimenting with plantings and increasing protections in areas, or at elevations, where trees may be more likely to survive. The spread of yellow-cedar decline represents a 'rear edge' in the ongoing cedar range shift, which presents its own set of management challenges, such as concerns about genetic diversity (Hampe & Petit, 2005). Rear edges are typically associated with the warmer, lower latitude portions of species range; in the case of yellow-cedar, it is an emerging climatic edge associated with warming, but in the higher latitude portions of its range (Table S1). While there is evidence of northerly progression of this mortality (Oakes *et al.*, 2014) which may continue, climate change-induced mortality may precede north to south for this species, contrary to general expectations for many species.

Conclusion

A gradually warming climate over the past century has caused cold-related damage and mortality in many forests due to phenological asynchrony and a decreasing proportion of precipitation received as snow. The loss of snow causes significant changes in soil conditions, especially in spring when soils are no longer insulated against fluctuating atmospheric temperatures. The north Pacific coast has significant areas on that winter freezing threshold, where only minimal amounts of warming are required to shift from snow- to rain-dominated winters; this loss of snow is associated with broad-scale species mortality. Approximately 7% of the range of yellow-cedar, a culturally, economically, and ecologically significant species, has experienced significant mortality (~70% basal area dead in impacted forests) in the past century due to a reduced of snow. Although little additional mortality has been noted in the past few years, potentially due to a series of cooler winters, projections are for up to 50% of the remaining areas currently below freezing to cross the winter-snow threshold in the next century, increasing exposure to potential mortality. The total percentage of area currently above-freezing temperature in winter and experiencing high mortality is variable (3.9–15.8%); complete, broad-scale extirpation in the near term (i.e., next 100 years) is not suggested at this time. The complex spatial pattern in this emergent climatically driven therefore appears to be a combination of a broad-scale mortality drivers (lack of snow) and fine-scale

heterogeneity in factors which either increase or decrease probability of mass die-offs. This phenomenon and pattern – root freezing and subsequent mortality as a result of climate warming – could be useful as a leading indicator for other global areas expected to cross the snow–rain temperature threshold later this century.

Acknowledgements

This work was partially supported by NSF Alaska EPSCoR award #OIA-1208927, the Alaska Coastal Rainforest Center, and the State of Alaska. We thank Marshall Murray for the use of his data on presence of yellow-cedar in California, Oregon, and Washington. We thank the editor, Dr. Heikki Hänninen, and an anonymous reviewer for their comments.

References

- Adam JC, Hamlet AF, Lettenmaier DP (2009) Implications of global climate change for snowmelt hydrology in the twenty-first century. *Hydrological Processes*, **23**, 962–972.
- Allen CD, Macalady AK, Chenchouni H *et al.* (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660–684.
- Anderegg WR, Berry JA, Smith DD, Sperry JS, Anderegg LD, Field CB (2012) The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *Proceedings of the National Academy of Sciences*, **109**, 233–237.
- Augsburger CK (2013) Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing. *Ecology*, **94**, 41–50.
- Beier P, Brost B (2010) Use of land facets to plan for climate change: conserving the arenas, not the actors. *Conservation Biology*, **24**, 701–710.
- Beier CM, Sink SE, Hennon PE, D'Amore DV, Juday GP (2008) Twentieth-century warming and the dendroclimatology of declining yellow-cedar forests in southeastern Alaska. *Canadian Journal of Forest Research*, **38**, 1319–1334.
- Breiman L (2001) Random forests. *Machine Learning*, **45**, 5–32.
- Buma B (2013) Don't give up just yet: maintaining species, services, and systems in a changing world. *Ethics, Policy, and Environment*, **16**, 1–4.
- Buma B (2015) Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere*, **6**, 1–15.
- Buma B, Barrett T (2015) Signs of disturbance disequilibrium and directional change in the world's largest temperate rainforest. *Global Change Biology*, **21**, 3445–3454.
- Cohen WB, Yang Z, Stehman SV *et al.* (2016) Forest disturbance across the conterminous United States from 1985–2012: the emerging dominance of forest decline. *Forest Ecology and Management*, **360**, 242–252.
- Dale VH, Joyce LA, McNulty S *et al.* (2001) Climate change and forest disturbance. *BioScience*, **732**, 723–734.
- D'Amore DV, Hennon PE (2006) Evaluation of soil saturation, soil chemistry, and early spring soil and air temperatures as risk factors in yellow-cedar decline. *Global Change Biology*, **12**, 524–545.
- D'Amore DV, Hennon PE, Schaberg PG, Hawley GJ (2009) Adaptation to exploit nitrate in surface soils predisposes yellow-cedar to climate-induced decline while enhancing the survival of western redcedar: a new hypothesis. *Forest Ecology and Management*, **258**, 2261–2268.
- Decker KLM, Wang D, Waite C, Scherbatskoy T (2003) Snow removal and ambient air temperature effects on forest soil temperatures in northern Vermont. *Soil Science Society of America Journal*, **67**, 1234–1242.
- DellaSala DA (2011) *Temperate and boreal rainforests of the world: ecology and conservation*. Island Press, Washington DC.
- Ellenwood JR, Krist FJ Jr, Romero SA (2015) *National Individual Tree Species Atlas*. FHET-15-01. U.S. Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team, Fort Collins, CO.
- Frenkel RE (1974) An isolated occurrence of Alaska-cedar (*Chamaecyparis nootkatensis* [D. Don] Spach) in the Aldrich Mountains, central Oregon. *Northwest Science*, **48**, 29–37.
- Groffman PM, Driscoll CT, Fahey TJ, Hardy JP, Fitzhugh RD, Tierney GL (2001) Colder soils in a warmer world: a snow manipulation study in a northern hardwood forest ecosystem. *Biogeochemistry*, **56**, 135–150.
- Gu L, Hanson PJ, Mac Post W *et al.* (2008) The 2007 eastern US spring freeze: increased cold damage in a warming world? *BioScience*, **58**, 253–262.
- Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rare edge matters. *Ecology Letters*, **8**, 461–467.
- Hannah L, Midgley GF, Millar D (2002) Climate change-integrated conservation strategies. *Global Ecology and Biogeography*, **11**, 485–495.
- Hannah L, Midgley G, Aneliman S *et al.* (2007) Protected area needs in a changing climate. *Frontiers in Ecology and the Environment*, **5**, 131–138.
- Hänninen H (2006) Climate warming and the risk of frost damage to boreal forest trees: identification of critical ecophysiological traits. *Tree Physiology*, **26**, 889–898.
- Hardy JP, Groffman PM, Fitzhugh RD *et al.* (2001) Snow depth manipulation and its influence on soil frost and water dynamics in a northern hardwood forest. *Biogeochemistry*, **56**, 151–174.
- Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation*, **142**, 14–32.
- Hennon PE, Shaw Hansen EM, III, CG, (1990) Dynamics of decline and mortality of *Chamaecyparis nootkatensis* in southeast Alaska. *Canadian Journal of Botany*, **68**, 651–662.
- Hennon PE, Trummer LM (2001) Yellow-cedar (*Chamaecyparis nootkatensis*) at the Northwest Limits of Its Natural Range in Prince William Sound, Alaska. *Northwest Science*, **75**, 61–71.
- Hennon PE, Wittwer DT (2013) Evaluating key landscape features of a climate induced forest decline. In: *Forest Health Monitoring: National Status, Trends, and Analysis* (eds Potter KM, Conkling BL), pp. 117–122. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.
- Hennon PE, D'Amore DV, Schaberg PG, Wittwer DT, Shanley CS (2012) Shifting climate, altered niche, and a dynamic conservation strategy for yellow-cedar in the North Pacific coastal rainforest. *BioScience*, **62**, 147–158.
- Hennon PE, McKenzie CM, D'Amore D *et al.* (2016) A climate adaptation strategy for conservation and management of yellowcedar in Alaska. USDA Forest Service GTR-917. 382 pp.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- Hobbs RJ, Cole DN, Yung L *et al.* (2009) Guiding concepts for park and wilderness stewardship in an era of global environmental change. *Frontiers in Ecology and the Environment*, **8**, 483–490.
- Inouye DW (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology*, **89**, 353–362.
- IUCN, UNEP-WCMC (2016) *The World Database on Protected Areas (WDPA)*. UNEP-WCMC, Cambridge, UK. Available at: www.protectedplanet.net (accessed 1 April 2016).
- Jackson ST, Betancourt JL, Booth RK, Gray ST (2009) Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences*, **106**, 19685–19692.
- Johnson EW, Ross J (2008) Quantifying error in aerial survey data. *Australian Forestry*, **71**, 216–222.
- Kareiva P (2014) New conservation: setting the record straight and finding common ground. *Conservation Biology*, **28**, 634–636.
- Kranabetter JM, McLauchlan KK, Enders SK *et al.* (2016) A framework to assess biogeochemical response to ecosystem disturbance using nutrient partitioning ratios. *Ecosystems*, **19**, 387–395.
- Krapek J, Buma B (2015) Yellow-cedar: climate change and natural history at odds. *Frontiers in Ecology and the Environment*, **13**, 280–281.
- Krist FJ Jr, Ellenwood JR, Woods ME *et al.* (2014) *National Insect and Disease Forest Risk Assessment*. FHET-14-01. U.S. Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team, Fort Collins, CO.
- van Lierop P, Lindquist E, Sathyapala S, Franceschini G (2015) Global forest area disturbance from fire, insect pests, diseases, and severe weather events. *Forest Ecology and Management*, **352**, 78–88.
- Matzner E, Borken W (2008) Do freeze-thaw events enhance C and N losses from soils of different ecosystems? A review. *European Journal of Soil Science*, **59**, 274–284.
- McLauchlan JS, Hellmann JJ, Schwartz MW (2007) A framework for debate of assisted migration in an era of climate change. *Conservation Biology*, **21**, 297–302.
- McLauchlan KK, Higuera PE, Gavin DG *et al.* (2014) Reconstructing disturbances and their biogeochemical consequences over multiple timescales. *BioScience*, **64**, 105–116.
- Meehl GA, Tebaldi C, Nychka D (2004) Changes in frost days in simulations of twenty-first century climate. *Climate Dynamics*, **23**, 495–511.
- Oakes LE, Hennon PE, O'Hara KL, Dirzo R (2014) Long-term vegetation changes in a temperate forest impacted by climate change. *Ecosphere*, **5**, 1–28.

- Oakes LE, Hennon PE, Ardoin NM *et al.* (2015) Conservation in a social-ecological system experiencing climate-induced tree mortality. *Biological Conservation*, **192**, 276–285.
- Ohmann JL, Gregory MJ (2002) Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, USA. *Canadian Journal of Forest Research*, **32**, 725–741.
- Paine RT, Tegner MJ, Johnson EA (1998) Compounded perturbations yield ecological surprises. *Ecosystems*, **1**, 535–545.
- Pauli JN, Zuckerberg B, Whiteman JP, Porter W (2013) The subnivium: a deteriorating seasonal refugium. *Frontiers in Ecology and the Environment*, **11**, 260–267.
- Perakis SS, Tepley AJ, Compton JE (2015) Disturbance and topography shape nitrogen availability and $\delta^{15}\text{N}$ over long-term forest succession. *Ecosystems*, **18**, 573–588.
- Perry RS (1954) *Yellow Cedar: Its Characteristics, Properties, and Uses*. For. Br. Bull. 114. Canadian Department of Northern Affairs and Natural Resources, Ottawa.
- Pickett STA, White PS (1985) In: *The ecology of natural disturbance and patch dynamics* (eds Pickett STA, White PS), Academic Press, San Diego, CA, USA.
- R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <https://www.R-project.org/>.
- Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH (2008) Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience*, **58**, 501–517.
- Rhoades CC, McCutchan JH, Cooper LA *et al.* (2013) Biogeochemistry of beetle-killed forests: explaining a weak nitrate response. *Proceedings of the National Academy of Sciences*, **110**, 1756–1760.
- Rigby JR, Porporato A (2008) Spring frost risk in a changing climate. *Geophysical Research Letters*, **35**, L12703.
- Running SW (2008) Ecosystem disturbance, carbon, and climate. *Science*, **321**, 652–653.
- Schaberg PG, Hennon PE, D'Amore DV, Hawley GJ (2008) Influence of simulated snow cover on the cold tolerance and freezing injury of yellow-cedar seedlings. *Global Change Biology*, **14**, 1–12.
- Seidl R, Fernandes PM, Fonseca TF *et al.* (2011) Modelling natural disturbances in forest ecosystems: a review. *Ecological Modelling*, **222**, 903–924.
- Shanley CS, Pyare S, Goldstein MI *et al.* (2015) Climate change implications in the northern coastal temperate rainforest of North America. *Climatic Change*, **130**, 155–170.
- SNAP (2009) Validating SNAP climate models. Scenarios Network for Arctic Planning. SNRAS Misc Pub No 2009-03. Available at: https://www.uaf.edu/files/snre/MP_09_03.pdf (accessed 1 April 2016).
- Stan AB, Maertens TB, Daniels LD, Zeglen S (2011) Reconstructing population dynamics of yellow-cedar in declining stands: baseline information from tree rings. *Tree Ring Research*, **61**, 13–25.
- Tierney GL, Fahey TJ, Groffman PM, Hardy JP, Fitzhugh RD, Driscoll CT (2001) Soil freezing alters fine root dynamics in a northern hardwood forest. *Biogeochemistry*, **56**, 175–190.
- Vitousek PM, Gosz JR, Grier CC, Melillo JM, Reiners WA, Todd RL (1979) Nitrate losses from disturbed ecosystems. *Science*, **204**, 469–474.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. This file contains the partial dependency plot from the random forest analysis relating mean winter temperature to probability of decline.

Table S1. This file contains a latitude by latitude summary of observed mortality and current area of Alaska yellow-cedar from 41° to 62° latitude, the entire natural range of the species.