Yellow-cedar: climate change and natural history at odds

A slow race is unfolding on the British Columbian and southeast Alaskan coast. The race involves Alaska yellow-cedar (*Callitropsis nootkatensis*), an ecologically, culturally, and economically important tree species that is uniquely susceptible to climate change due to its natural history and ecological strategies. In the southern and coastal portions of its range, yellow-cedar is dying rapidly due to a warming climate; massive cedar mortality (observed in an area > 200 000 ha; Figure 1) has occurred and continues to occur. At the same time, on the edge of its northern range, this species is slowly expanding into suitable habitat and more favorable climes, with no major barriers to northern expansion immediately in sight. As the climate continues to warm, the forest as a whole could look very different, depending on how this race between southern range contraction and northern range expansion proceeds.

Yellow-cedar is a member of the cypress family (Cupressaceae), an ancient group that contains the tallest (coast redwood), largest (sequoia), and second oldest (Alerce) trees on the planet. Extant members are found in a variety of habitats on every continent except Antarctica (with likely fossil evidence there). Yellow-cedar apparently speciated relatively late, splitting from the junipers 50–75 million years ago, then dispersing to North America from Asia (Mao *et al.* 2012). It is one of the slowest growing conifers in the Pacific Northwest, and most at home in sparsely treed, boggy sites (known as muskegs) with poorly drained soils and little competition for light. Yellow-cedar invests a substantial amount of energy into defensive (including antifungal) compounds, giving it surprising durability despite the extremely wet, nearly saturated conditions where it grows – characteristics that preclude the occurrence of most other tree species. The wood has been used for millennia by Alaskan and British Columbian Native peoples, as building material and to make canoes, and is still prized for outdoor furniture and framing. Fallen limbs and whole trees retain their distinctive chemistry for decades after death, producing unusually long-lasting debris on the wet forest floor (Kelsey *et al.* 2005).

Specialization in muskegs and other poorly drained soils is the key to yellow-cedar's success. Nitrogen (N) limitation is common throughout the temperate zones, and is exacerbated further by wet soils. Like most of the Cupressaceae, yellow-cedar preferentially takes up nitrate (NO_3^-), which is produced in the shallow, unsaturated upper few centimeters of the soil profile (Krajina *et al.* 1973); however, internal electrochemical charges associated with this type of nutrient uptake must be balanced in some fashion. One way to achieve this balance is to take in calcium (Ca_2^+) – yellow-cedar accumulates this nutrient far above its metabolic needs, after which the calcium is transported to the foliage and, ultimately, into the upper layers of soil as detritus from "foliage rain". This results in an advantageous, self-promoting positive feedback as increased soil pH (from the increased calcium concentration) promotes nitrification, increasing N availability in the shallow upper portions of these slowly cycling soils (D'Amore *et al.* 2009). A second pulse of nitrification occurs briefly in the spring, as microbial cells in the soil burst during rapid freeze–thaw cycles. The ability to take advantage of this surge in available N requires an aggressive, but potentially risky, growth strategy. Yellow-cedar becomes photosynthetically active earlier in the spring than the other tree species in the region, an opportunistic response to this temporally limited, shallow N pool (D'Amore *et al.* 2009). During these times, yellow-cedar remains photosynthetically active at low air temperatures, even slightly below freezing (Schaberg *et al.* 2011). Overall, these strategies are well-suited for cool, wet, N-limited landscapes.

Unfortunately, specialization may result in dependency on a narrow range of environmental conditions, and vulnerability when those conditions change. In the case of yellow-cedar, both shallow rooting (due to water-logged soils and the need to exploit shallow N sources) and physiological adaptations for early-spring growth expose trees to potential freezing injury should soil temperatures dip too low (Schaberg *et al.* 2011). This isn't a problem if there is an ample snowpack that lingers late into spring, as the area beneath the snow is buffered from cold air temperatures until long after the threat of a deep freeze is past (incidentally, late snowpack also protects seedlings from Sitka and Columbian black-tailed deer [*Odocoileus hemionus sitkensis* and *O h columbianus*], which appear to target cedar for winter browse). As average temperatures have risen following the Little Ice Age (which ended during the mid-19th century CE), and more rapidly with anthropogenic atmospheric carbon dioxide accumulation, rain has replaced snow throughout much of the year, reducing that insulating blanket of snow in late spring (Hennon *et al.* 2012). Consequently, yellow-cedars are out of sync with their temperature environment, and their roots – shallow and physiologically active – become exposed to spring freezing events (when they do succeed in better drained soils, it is because their roots are deeper). It doesn't take much to cause root mortality; soil temperatures of –5°C are low enough. If a sufficient number of roots are killed in one year, or over a few successive years, the entire tree dies. Because of this, wide swaths of dead cedars extend across southeast Alaska and into neighboring British Columbia (Figure 1a), with mortality rates higher than 70% in some areas (Hennon *et al.* 2012).

Leave the heart of concentrated cedar mortality and

travel a couple of hours northeast by float plane, or a bit longer by boat, and the situation looks quite different. Slightly colder average temperatures translate into more snow, and a snowpack that lingers longer. The same spruce–hemlock (*Picea–Tsuga*) forests dominate as in the south, with muskegs interspersed wherever the slope evens out or bedrock cups runoff into wet pockets. Yet yellow-cedar is rarely seen here, and most people don't even know it's there. It's not entirely absent – small, isolated groups are scattered about, seemingly at random. Some spots have upwards of 40 mature giants, others five, and in one case, a lonely cedar stands all by itself alongside an old mining ditch (Figure 1b). This is the leading edge of the other part of the race, the race into suitable habitat. These cedars appear to be new arrivals at the leading edge of an ongoing, slow migration from beyond the southern end of the Cordilleran Ice Sheet during the Last Glacial Maximum, hypothesized glacial refugia along the outer coast of southeast Alaska and Queen Charlotte Islands (Carrara *et al.* 2007), or both.

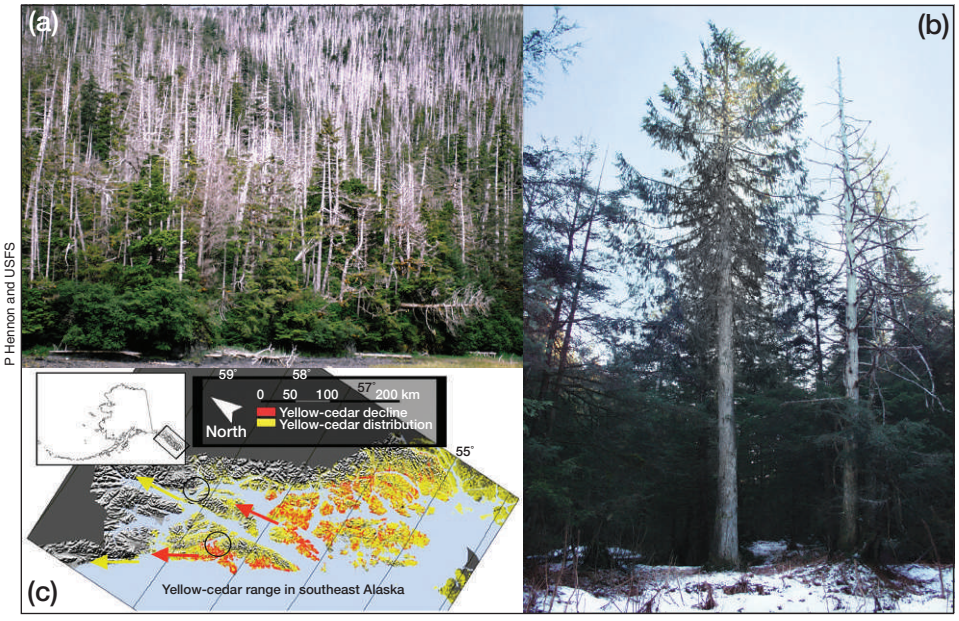

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Figure 1. *Yellow-cedar (*Callitropsis nootkatensis*) decline/expansion and map of general region. (a) Hillside near Sitka, Alaska, dominated by dead and dying yellow-cedar (with some residual spruce [*Picea*]) from freezing mortality as a result of shallow rooting and low snowpack. (b) On the other side of the species' climatic range, range-edge populations are slowly spreading north. The "lonely cedar" growing near Douglas, Alaska, is shown (coring evidence indicates that the tree sprouted in the year 1891). No other individuals are known within several kilometers. (c) A map of yellow-cedar distribution and decline in southeast Alaska, with the picture locations (circles) and migration/decline advance (arrows).*

Yellow-cedar is again suffering because of its biology, however; a number of factors combine to keep its migration at a near-glacial pace. Only about one-quarter of its seeds are viable, and they tend to be heavy; this likely enables them to establish on thicker organic soils, but also limits their estimated dispersal distance to under 120 m (Burns and Honkala 1990). In an archipelago environment where muskegs, although plentiful, are scattered, dispersal is a slow and jerky affair. Chance long-distance dispersal, when it occurs, is probably a product of strong fall and winter winds from the south, concurrent with the release of viable seed crops. Some of these seeds may make it to muskeg sites, establishing a new population, and pushing the range edge that much farther. Layering (asexual reproduction) is fairly common in muskegs, and this may serve to fill in a stand after a successful long-distance dispersal event, though slowly (Hennon *et al.* 2012). Forest blowdown may also provide germination sites, allowing for the occasional establishment of yellow-cedar in drier upland locations. We know relatively little about yellow-cedar's spread; for instance, how do these pioneers interact with preexisting plant communities? Many questions remain regarding dispersal and establishment along the leading range edge, which are key in predicting the ultimate impacts of climate change on the species.

Standing at that advancing edge today, though, things look healthy. The scattered yellow-cedar populations appear to be new and growing – there are few dead individuals, and ample regeneration. But climate models make it clear that the current snowpacks that maintain favorable environmental conditions are quickly diminishing (Shanley *et al.* 2015). Topography will offer some respite, as sheltered and high-elevation areas will retain snow, and for now well-drained soils appear to protect cedar from the cold. Nonetheless, available habitat will certainly be drastically reduced. This is where humans are considering joining the race, potentially implementing policies of assisted migration and conserving yellow-cedar in safe sites remaining across its range, such as high-elevation locations or pockets where snow lingers due to cold air drainage. Experimental plantings by the US Forest Service near the northern range edge grow well, and land managers are considering further aiding this species in its slow march north. For now, at least, the race is on.

References

Please see WebReferences

John Krapek
School of Natural Resources and Extension, University of Alaska Fairbanks, Fairbanks, AK
Brian Buma*
Department of Natural Sciences, University of Alaska Southeast, Juneau, AK
**(brian.buma@uas.alaska.edu)*