



LIMBER PINE'S WILD RIDE WITH CLIMATE: UP, DOWN, AND ALL AROUND

Text and Photos by Constance I. Millar

Despite its widespread distribution, broad ecological influence, and respectable longevity, limber pine (*Pinus flexilis*) remains little known next to its more charismatic cousins, whitebark pine (*P. albicaulis*) and Great Basin bristlecone pine (*P. longaeva*). A mountain species by nature, limber pine inhabits the subalpine zone across much of temperate western North America. In California, limber pine occurs sporadically in the mountains of southern California, the southwest Sierra Nevada, and the Great Basin (GB) portions of California east of the Sierra Nevada crest. Its range continues to the east, across the high mountains of the GB, where it extends from the woodland conifer community through the uplands to form the upper treeline. Limber pine's wide distribution in the GB, often as the only high-elevation conifer, means that it has critical ecological significance, sheltering and supporting the subalpine biome.

Limber pines can grow to 2,000 years old, and their dead wood can persist on the ground for millennia. These factors allow scientists to use limber pine to unravel climate and ecology of the past. Our recent and ongoing studies of limber pine's response to past and present climate change offer some insights that challenge generally accepted assumptions, and may be helpful for the future management and conservation of resilient subalpine forests in California and beyond.

Above: Limber pine is reproducing not only at and above upper treeline but also at middle elevations, as in basins near Crooked Creek in the White Mountains of California.

Beyond its role as a keystone species and indicator of climate history, limber pine—with its warm, wine-red bark and gnarled, twisted forms cast against stark, open landscapes—provides a worthy aesthetic equal to the better-known bristlecone pine.

Taxonomically, limber pine is a five-needled “soft pine” (Subgenus *Strobus*). At first appearance it is easy to confuse limber with whitebark and western white pines. The only reliable field characteristic for distinguishing it from its subalpine congeners—whitebark, western white, and bristlecone pines—is the seed cone, which has an intact structure with stout scales and large seeds that have a highly reduced wing. The bark is often plate-like in old-growth trees, and the crown often spreads at the top, and can take striking wind-blown and asymmetric forms. The seeds are distributed by birds, primarily Clark's nutcrackers (*Nucifraga columbiana*), while those of the related species that share its distribution—whitebark pine excepting—are wind dispersed.



The seed cones are the only morphological characteristic that allows limber pine to be distinguished from related pines. Note the stout, elongated cone when closed (longer and thinner than whitebark pine, sturdier than western white pine), the thick bracts on the open cone (thicker than western white pine), and the persistence of the cone on the stem when mature (whitebark pine cones are torn apart by Clark's nutcrackers on the stem).

ECOLOGY AND CLIMATE

In our region (California and the Great Basin), old-growth stands of limber pine are generally sparse, with little understory growth. In the mountains of Southern California, limber pine has a minor role in mixed conifer forests. The species becomes more prominent in the southern Sierra Nevada, where it occurs with whitebark pine, lodgepole pine (*P. contorta*), and/or foxtail pine (*P. balfouriana*). In the White Mountains, limber pine mingles with bristlecone pine. The species can also be found in several smaller mountain ranges east of the Sierra Nevada in California, including the Glass Mountains, Bodie Mountains, and Sweetwater Mountains. Limber pine grows throughout the sub-alpine zone to the upper forest treeline, although where it occurs with bristlecone pine the latter extends to higher elevations. In the interior GB, limber pine occurs across the “cool” mountain zones, often as the sole upland conifer above pinyon (*P. monophylla*)/juniper (*Juniperus osteosperma*) woodlands.



The distribution of limber pine in the Great Basin (within the white lines; large map), and range-wide distribution (inset).

As might be inferred from this sketch, limber pine tolerates dry and warm interior mountain climates, with summer rain being an important element. Long Mediterranean summers without moisture relief push limber pine to competitive disadvantage. Similarly, where winters are long with deep snowpacks, limber pine yields to whitebark pine in the Sierra Nevada, Englemann spruce (*Picea engelmannii*) in eastern Nevada, or firs (*Abies* spp.) in the northern GB ranges. Within the GB, bristlecone pine has the most similar climatic requirements to limber pine. Given that bristlecone pine generally out-competes limber pine on carbonate and quartzite substrates, in the mountain ranges where those soils are extensive bristlecone pine dominates. Whereas the opposite is true for the ranges dominated by non-carbonate substrates such as granite, which favor limber pine.

Left: Old-growth limber pine with strip-bark stem and spiral grain growing on barren volcanic soils on Glass Mountain, Mono County in California.

LIMBER PINE AS A CLIMATE-STUDY SPECIES

Much of what is known of limber pine's ecology and genetics comes from studies in the Rocky Mountain part of its range. More than a decade ago, to expand our understanding of the species across its range, my research team at the Pacific Southwest Research Station of the U.S. Forest Service chose limber pine in the GB as a focal species to study for its responses to climate change, including both natural historic variability and ongoing human-mediated effects. Why choose limber pine? Not only is it important to understand limber pine's ecology in itself, given its role in subalpine forests, but we contend that limber pine in the GB ranges is a useful proxy (indicator) for potential future conditions of the subalpine forests of the Sierra Nevada. The many mountain ranges in the GB—653 overall (Charlet 1996), including 37 that have peaks reaching above 10,000 feet (Grayson 2011)—provide useful redundancy for testing hypotheses. Further, these mountains experience a wide range of climates similar to, but usefully different from, the Sierra Nevada, thus providing a diversity of potential “climate futures” to study in a space-for-time context. In addition, fuel in the subalpine zone of the semi-arid ranges of the GB is sparse and landscape fires infrequent. With lack of fire and cool-dry conditions, limber pine dead wood can be preserved on site for many millennia, providing useful information about past conditions.

We use a variety of methods to study limber pine's historic responses to climate variability as well as the effects of current climate change. Primary among these is tree-ring analysis, which involves extracting a thin cross-sectional core of wood with an increment borer; this reveals the rings of the tree—alive or dead—extending from the pith (center of the stem) to the outer bark. From these cores we can determine the age of live trees and, using cross-dating methods, work back in time to estimate the age of dead wood. Such dating is approximate, because the pith can be missing due to heart-rot, and erosion can remove outer rings near the bark.

In addition to determining tree ages, at each location we evaluate the relative growth of all annual rings in every tree sampled (secondary cambial growth in trees) and develop what are called “standard tree-ring chronologies” for each population. From these, we assess the climate variables, derived from instrumental weather stations in the region of the limber pine sites, extending back to the late 1800s, that best correlate with limber pine ring growth. Limber pine growth

is complexly correlated to instrumental climate data, with smallest rings occurring when growing season temperatures are either very high or very low with low precipitation, and largest when growing season temperatures are warm and precipitation is high.

For understanding range shifts at local to regional scales in response to climate, we add demographic methods to tree-ring approaches, which enable us to know birth and death dates. With these combined approaches, we can estimate density of tree stems and cohort ages for current conditions and also tree densities in the past. We correlate data with climate information, once again, from instrumental weather stations, to infer modern responses of limber pine recruitment and death. For historic conditions we are lucky that many studies have reconstructed pre-historic climates in the GB, using inferences from proxies as diverse as glacial moraines, lake sediment cores, paleo-historic pollen and macro-fossil distributions, packrat middens, and tree-ring estimations. These provide climate analogs for past centuries and millennia that replace the direct observational values from instrumental records, which extend at best only 140 years into the past. Interestingly, correlations of limber pine recruitment suggest that the best annual conditions for stem growth also favor germination and seedling establishment.

MOUNTAIN CLIMATES AND SPECIES RESPONSE—NOT ALWAYS AS EXPECTED

“Mountain species will shift up in elevation as temperatures warm.” Some version of this statement is so widely accepted that it has become a truism about climate-change effects. Tied to this is the projection that as mountain species shift upwards in pace with changing temperatures they eventually “run out of space at the top of mountains and become extirpated.” An early and prominent example of this projection comes from the study of Hayhoe et al. (2004), who modeled California climate at 2020 under diverse emission scenarios, and projected 75–90% loss of alpine and subalpine forest vegetation in California as a result of “elevational squeeze.”

The basis for these assumptions and modeling projections derives from the phenomenon commonly experienced by mountain visitors that temperatures cool as one moves to higher elevations. Under specified standard conditions, this physical process is described as the “atmospheric lapse rate,” in which, depending on location, the temperature declines between 6.5°C and



Our colleague, John King, coring an old-growth limber pine on Mount Grant in the Wassuk Range in Nevada.

10°C with each one kilometer increase in elevation. At long prehistoric time scales (millennia), movements of many mountain conifers have been documented to follow expected climate patterns (Huntley and Webb 1989). Similarly, as anthropogenic warming accelerates, many mountain tree species have been found to be shifting their ranges upward (e.g., Beckage et al. 2008; Lenoir et al. 2008).

At closer inspection, however, the enormous topographic diversity of mountain ranges, from the broad scale of valleys and peaks to the more localized scale of talus slopes and rock boulders, dictates that the atmospheric lapse rate is commonly broken. Topo- and micro-climatic processes, such as cold-air drainage (creating inversions), wind funneling, variability in solar radiation, and many other processes, affect local air temperatures and influence biotic response. Further, the size and mobility of mountain species has much to do with how individuals react to climate: For instance, a tall tree engages with regional atmospheric conditions while a stunted krummholz pine (“pruned” and shaped by wind and cold) or an alpine cushion plant experiences a very different weather environment. Thus, mountain species should be expected to

respond to climates that they actually encounter rather than theoretical conditions based on standard processes such as lapse rates or generalized regional conditions.

RESPONSES OF LIMBER PINE TO PAST AND PRESENT CLIMATE

Given the potential for mountain species to respond in more ways than simply shifting uphill or going extinct, we set out to investigate the diverse avenues that limber pine has taken or might take to respond adaptively to climate change. And the species has given us some surprising results. Below I summarize a few of our relevant findings.

Movement Up With Warming (But With a Twist)

In GB mountain ranges, there are locations where limber pine seedlings are establishing above the current upper forest border, as the common assumption would predict for warming conditions. However, there are some unexpected elements associated with this pattern (Millar et al. 2015, Smithers et al. 2017). First, the locations where limber pine seedlings are recruiting above current treeline are extremely rare, especially given the abundance of environments and extensive high elevation slopes that appear suitable for such upward expansion. Second, there seems to be—with an exception—no obvious environmental or climatic pattern to where these locations for recruitment occur. The exception is, in mountains where both bristlecone pine and limber pine occur, that seedling recruitment above current treeline often (but not always) occurs where ancient dead bristlecone pine stems remain above the current treeline.

Another surprise: In these ranges, limber pine is leap-frogging above bristlecone pine; that is, limber pine seedlings are more abundant above the current treeline than bristlecone pines. Finally, whereas it might be expected that recruitment upslope would correlate with warming over the past century, in fact, it has been episodic, with a pulse of seedlings dated from 1963 to 2000. This late 20th century interval correlates with a period of warm-but-not-hot temperatures in the growing season, and abundant summer/autumn precipitation, apparently conducive to seedling establishment and growth. These conditions have been less frequent over the last 20 years as multi-year droughts coincided with ongoing warming that created unfavorable conditions for seedlings to establish.

What is the fate of leap-frogging limber pine relative to bristlecone pine? From our current vantage point, we cannot predict the long-term conditions above current

treeline. The limber pine surge might be transient; bristlecone pine might catch up; or it might leap over limber pine (bird distribution favors limber pine early in the race, but wind-dispersed bristlecone pine might dominate later); or something very different might occur. What we do know from observation is that both species are currently recruiting uphill in very limited alpine locations, and that healthy subalpine forests of both species span across more than 3,000 feet of elevation. At present, both species appear hale and hearty in the ranges where they have been common in the past, especially considering other demographic responses, as discussed in the following section.

Moving Out at Mid-Elevations and Down in Low-Elevation Ravines

Many studies that investigate the response of mountain species to climate change focus primarily on the upper elevation range of those species. In contrast, our studies also look at the dynamics of limber pine at other parts of its elevation range. This provides a different perspective to what is occurring “at the top.” In the same study where we evaluated seedlings above the current treeline, we also estimated ages and densities of limber pine at mid- and low-elevations (Millar et al. 2015). Interestingly, we found that the species is still reproducing at these locations, if at lower densities than above treeline, and during the same late 20th century time/climate period. At mid-elevations, we found that the locations where seedlings established beyond the forest edges occur most often in sagebrush steppe basins. We inferred that temperature inversions that occurred historically in these locations and restricted seedling establishment were being disrupted by warming, allowing recruitment into these shrub habitats. Once again, the ages of these seedlings coincided with the cohort above current treeline.

Perhaps most surprising to us was finding limber pine seedlings establishing *below* the current forest border. We found them most often in narrow ravines, often north-facing, and once again with similar ages to the other pulses of recruitment. This low-elevation phenomenon fascinated us, and we took it up in a subsequent study (Millar et al. 2018a), investigating lim-



Limber pine is reproducing not only at and above upper treeline but also at middle elevations, as in basins near Crooked Creek in the White Mountains of California.

ber pines at low elevations across 50 mountain ranges of the GB. We were surprised to find a significantly disproportionate abundance of limber pines distributed in low ravines. These were often extra-marginal to the main part of the species distribution, which occurred on high-elevation, open slopes far above the ravines. Unexpectedly, seedlings were thriving under deep, dark, and humid riparian canopies of willow (*Salix* spp.), cottonwood (*Populus* spp.) and water birch (*Betula occidentalis*); mature limber pines extend



Surprisingly, limber pine is also reproducing in the dense shade of lowland riparian vegetation, as here under water birch (*Betula occidentalis*) in the Toquima Range in Nevada, where damp, organic soils usually exclude pine seedlings.

above the crowns of these gallery forests. From a network of datalogger observations and estimates from the PRISM climate model (Daly et al. 1994), we assessed that although, as expected, these locations were warmer than the uplands, humidities are higher under the riparian canopies, soil moisture is higher than along slopes, and wind desiccation less. From these and other investigations, we conjecture that low-elevation ravine sites have served prehistorically as climate refugia for limber pine in the GB and might be important locations for the species to persist in the warming future. As such, climate adaptation and conservation efforts would be wise to consider these unexpected locations for protection (Morelli et al. 2016).

Limber Pine Moves All Around, But Bet On North

The Wassuk Range of western Nevada looms over Walker Lake to its highpoint of 11,285 feet atop Mount Grant. In contrast to the blue waters shimmering below, the range's upper slopes are arid and mostly barren of trees. Above the pinyon-juniper zone, sparse stands of limber pine grow on northward aspects. Abundant dead stems of large limber pines are scattered on these slopes and, unexpectedly, on all other aspects, including across entire watersheds where there are now no living limber pines. Because the wood of these relict stems is well preserved in the dry climate and fire-free landscape, we were able to collect and date, using tree-ring methods, more than 500 stems from across the range's high slopes (Millar et al. 2018b). These dated continuously from the present back to 1983 BCE (before Common Era), thus yielding a record of more than 4,000 years. From these stems we evaluated two distinct types of responses to prehistoric multi-century climate periods, including the Late Holocene Dry Period, Medieval Climate Anomaly, Little Ice Age, and the contemporary warming century.

First we evaluated growth of annual rings across the millennia from limber pines on all slopes and found growth correlated to the same weather conditions as in our other studies of modern stands. Importantly, growth also correlated to the multi-century climate intervals in expected ways—that is, higher growth during warm-wet periods, and lower growth during hot-dry or cold-dry periods.

Such associations with climate periods was not the case, however, for our demographic evaluations. Because we had so many dated stems, we could fairly assess the presence, absence, and relative abundance of stems at different locations across 4,000 years. We found, first, that despite high climate variability, there was no evidence for elevation shifts up or down over time, despite the existence of abundant areas on the high plateaus where pines could have migrated. Second, although there were periods of colonization and extirpation on slopes of different aspects across the millennia, there was no significant correlation with the prehistoric climate periods. Importantly, only on the north slopes did pines persist continuously—without extirpation and in denser stands—across the 4,000 year record.

From these results we infer that non-climatic effects, such as seed dispersal by Clark's nutcrackers and the presence or absence of essential ectomycorrhizal fungi, likely play an important role in where and when limber pines can grow, trumping influences of climate. We conclude that north slopes, with their higher humidities, lower solar radiation, higher soil moisture, and denser shrubby vegetation, support limber pine growth and persistence across centuries, even during periods when the climate might otherwise appear less conducive for the species. Thus, north-facing slopes might also serve as long-time refugia for limber pine in GB mountains, and, along with low ravine sites, could be evaluated for protection in climate-adaptation and conservation efforts.

A FINAL UNEXPECTED OUTCOME: LIMBER PINE AND BARK BEETLES

Over the last two decades, bark beetle epidemics in pine forests throughout the West have startled biologists and the public alike for their magnitude and severity. In the Sierra Nevada, tree mortality



Left: Limber pine growing on north slopes above Walker Lake in the arid Wassuk Range, where stands of the species have found refugial conditions despite varied climates of the past 4,000 years.

in subalpine forests was not as severe as in mountain regions elsewhere in the western United States, and pockets of mountain pine beetle outbreak on limber pine and whitebark pine were relatively small. Limber pine was affected in the 1986-1992 drought (Millar et al. 2007), while whitebark pine was attacked in the 2007-2013 drought (Millar et al. 2012). We used tree-ring and demographic approaches to evaluate the effects of the beetle outbreaks on the two species. In both cases we were surprised to find that the beetles killed fewer than 70% of the large trees in affected stands. The silvical thinning that resulted actually provided better growth conditions for the trees, enabling them to survive subsequent pine beetle attacks. Trees that succumbed to beetle attack appeared to have been poorly adapted genetically to the warm-dry conditions of the 20th and 21st centuries but had been better adapted to the cold-wet conditions of the Little Ice Age (LIA) centuries (~1450-1900). The opposite occurred for trees that survived; they had grown poorly during the LIA but grew significantly better under the more recent warming climates. Finding the same result in both species, we concluded that the bark beetle mortality actually improved the silvical and genetic composition of the forests, providing them with greater adaptation to future warming. This finding, of course, would not pertain if no trees survived the outbreak.

CONCLUSIONS

Our studies with limber pine have provided insights into how subalpine native pines respond to climate change. These included not only expected shifts up in elevation with warming, but many surprising and unexpected responses as well. These findings remind us that in scientific research, as in conservation, we should look beyond the expected—biology often throws a curveball into our assumptions. From the findings about limber pine, we might anticipate designating and protecting refugia in such places as low-elevation ravines and north-aspect slopes. Further, while dying trees are not pretty to the human eye, and dead trees can (for a period of time) promote fire and other hazards, it is valuable to consider the role of native insects in promoting adaptation to future conditions in long-lived trees. These and other surprises, and their attendant conservation implications, will surely continue to arise as scientists probe more deeply into the actual—rather than assumed—responses of trees to climate change.

Acknowledgments

I thank David Loeb, Ron Lanner, and Jonathan Nesmith for critical review of the draft manuscript.

REFERENCES

- Beckage, B., B. Osborne, D.G. Gavin, C. Pucko, T. Siccama, and T. Perkins. 2008. A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proceedings of the National Academy of Sciences* 105: 4197-4202.
- Charlet, D.A. 1996. *Atlas of Nevada conifers*. A phytogeographic reference. University of Nevada Press, Reno, Nevada. 320 pp.
- Daly, C.R., R.P. Neilson, and D.L. Phillips, D.L. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *Journal of Applied Meteorology* 33: 140-158.
- Grayson, D.K. 2011. *The Great Basin. A natural prehistory*. University of California Press, Berkeley, California. 418 pp.
- Hayhoe, K., D. Cayan, C.B. Field, P.C. Frumhoff, E.P. Maurer, N.L. Miller, S.C. Moser, S.H. Schneider, K.N. Cahill, E.E. Cleland, L. Dale, R.P. Drapek, R.M. Hanemann, L.S. Kalkstein, J. Lenihan, C.K. Lunch, R.P. Neilson, S. Sheridan, and J.H. Verville. 2004. Emissions pathways, climate change, and impacts on California. *Proceedings of the National Academy of Sciences* 101: 12422-12427.
- Huntley, B., and T. Webb III. 1989. Migration: species' response to climatic variations caused by changes in the earth's orbit. *Journal of Biogeography* 16: 5-19.
- Millar, C.I., R.D. Westfall, and D.L. Delany. 2007. Response of high-elevation limber pine (*Pinus flexilis*) to multiyear droughts and 20th-century warming, Sierra Nevada, California, USA. *Canadian Journal of Forest Research* 37: 2508-2520.
- Millar, C.I., R.D. Westfall, D.L. Delany, M.J. Bokach, A.L. Flint, and L.E. Flint. 2012. Forest mortality in high-elevation whitebark pine (*Pinus albicaulis*) forests of eastern California, USA; influence of environmental context, bark beetles, climatic water deficit, and warming. *Canadian Journal of Forest Research* 42: 49-765.
- Millar, C.I., R.D. Westfall, D.L. Delany, A.L. Flint, and L.E. Flint. 2015. Recruitment patterns and growth of high-elevation pines in response to climatic variability (1883–2013), in the western Great Basin, USA. *Canadian Journal of Forest Research* 45: 1299-1312.
- Millar, C.I., D.A. Charlet, R.D. Westfall, J.C. King, D.L. Delany, A.L. Flint, L.E. Flint. 2018a. Do low-elevation ravines provide climate refugia for subalpine limber pine (*Pinus flexilis*) in the Great Basin, USA? *Canadian Journal of Forest Research*. 48(6): 663-671.
- Millar, C.I., D.A. Charlet, D.L. Delany, J.C. King, and R.D. Westfall. 2018b. Shifts of demography and growth in limber pine forests of the Great Basin, USA, across 4000 years of climate variability. *Quaternary Research* 1-14.
- Morelli, T.L., C. Daly, S.Z. Dobrowski, D.M. Dulen, J.L. Ebersole, S.T. Jackson, J.D. Lundquist, C.I. Millar, S.P. Maher, W.B. Monahan, K.R. Nydick, K.T. Redmond, S.C. Sawyer, S. Stock, and S.R. Beissinger. 2016. Managing climate change refugia for climate adaptation. *PLoS One* 11: e0159909.
- Smithers, B.V., M.P. North, C.I. Millar, and A.M. Latimer. 2017. Leap frog in slow motion: Divergent responses of tree species and life stages to climatic warming in Great Basin subalpine forests. *Global Change Biology* 24: e442-e457.