



## Differences in functional ecology of two western North American ‘five-needle’ white pines in treeline communities

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Whitebark pine (*Pinus albicaulis*) and limber pine (*Pinus flexilis*), related five-needled white pines (*Pinus* subgenus *Strobus*, section *Quinquefoliae*, subsection *Strobus*), are distributed throughout the mountains of the western United States and Canada. Whitebark pine ranges from about 36° to 56° N latitude, and limber pine ranges from about 34° to 52° N latitude. Both pines are tolerant of harsh sites, including poor soils and arid conditions, but whitebark pine inhabits colder sites and is restricted to high elevations, and limber pine occupies a broader elevational range and has more drought-resistance. The seeds of both pines are dispersed primarily by Clark’s nutcrackers (*Nucifraga columbiana*), which often cache seeds at treeline and in tundra. In the Rocky Mountains, both pines are components of treeline communities but differ in growth form and foliage density and thus potential capacity to serve a facilitation function. Our previous studies identified different ecological functions or roles assumed by trees in Rocky Mountain treeline communities: isolated solitary tree, most windward tree of a tree island (potential tree island “initiator”), satellite tree (sheltered by a tree island), or tree island component (leeward of windward tree). We examined whether whitebark and limber pine differ in ecological functions in treeline communities. Whitebark and limber pine primarily co-occur with Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) at treeline, and both pines have higher abundance at treeline east of the Continental Divide. In treeline communities broadly sampled from 42° to 53° N latitude, whitebark pine was the majority solitary conifer in 9 out of 10 treeline study sites and had the highest representation within tree islands at 8 of 10 study sites. Whitebark pine was the most frequently occurring windward conifer in tree islands at half of the study sites, and its proportional abundance as a solitary tree predicted its proportional abundance as a windward conifer. Limber pine, in contrast, was rare at treeline at northern latitudes but more common in the arid southern Rocky Mountains. We studied treeline communities in Rocky Mountain National Park, both east and west of the Continental Divide in 19 study sites. Limber pine was found only east of the Divide and varied in prevalence from 0% to 97.6% of trees within a study site. It most frequently occurred as a satellite or solitary tree and less frequently as a windward tree than expected by its representation as a solitary tree. We found a relationship between the proportion of limber pine at our treeline sites and the distance to a subalpine limber pine seed source, likely resulting from seed dispersal by nutcrackers against prevailing winds. In sum, tolerance of harsh, windy conditions by both pines, coupled by avian seed dispersal, leads to their prevalence as solitary trees in treeline communities east of the Continental Divide. Whitebark pine’s denser morphology likely facilitates establishment of conifers to its lee. Limber

pine's drought tolerance enables it to survive well on windswept ridges and slopes—which have earlier snowmelt dates—and may lead to increasing prevalence with climate change.