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DIFFERENCES IN FUNCTIONAL ECOLOGY OF TWO WESTERN NORTH AMERICAN ‘FIVE-NEEDLE’ WHITE PINES IN TREELINE COMMUNITIES

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Introduction

The alpine-treeline ecotone (ATE) is transitional between forest timberline (upper limit of subalpine forest) and treeline (upper limit of tree growth) (e.g., Malanson et al. 2007). Within the ATE, conifers assume a continuum of wind-impacted growth forms and comprise a mix of tree island patches and scattered individual trees. Tree growth in the ATE is limited by air and root zone temperatures (Körner and Paulsen 2004); thus the ATE is sensitive to climate change and has historically advanced and retreated in elevation (Holtmeier and Broll 2019). Despite increasing global temperatures, as of 2006 only 52% of treelines had advanced in elevation (Harsch et al. 2009), indicating complexity in treeline dynamics. Recent studies suggest that treeline advance may be limited by topography, moisture, and light exposure; facilitated locally by nurse objects and protective microsite; and inhibited or facilitated by species-specific interactions or adaptations (e.g., McIntire et al. 2016, Pyatt et al. 2016, Brodersen et al. 2019, Shemesh et al. 2019, Malanson et al. 2019).

We propose certain ATE species have adaptations and interactions that lead to different tolerances and ecological functions and may potentially influence treeline response to climate warming. For example, in the arid Great Basin, USA, drought-tolerant limber pine (*Pinus flexilis*), which depends on avian seed dispersal, is advancing upslope, with greater densities of regeneration above timberline than associated Great Basin bristlecone pine (*Pinus longaeva*) (Smithers et al. 2018).

Conifer functional roles at treeline and high elevation ‘five-needle’ white pines

Studies in Rocky Mountain ATE communities indicate distinct ecological or functional roles assumed by conifers within and adjacent to tree islands (e.g., Resler and Tomback 2008, Tomback et al. 2016a, Sindewald et al. 2020, 2023). See **Fig. 1** for descriptions.

Limber pine and *whitebark pine* (*Pinus albicaulis*) are western, North American ‘five-needle’ white pines (Pinaceae, subgenus *Strobus*, section *Quinquefoliae*, subsection *Strobus*) that may facilitate treeline advance (**Fig. 2**). Whitebark pine ranges farther north, from ~36° to 56° N latitude, and limber pine from ~34° to 52° N latitude (**Fig. 3**) (Tomback and Achuff 2010). Both are hardy conifers that experience ‘directed seed dispersal’ through the caching behavior of Clark’s nutcrackers (*Nucifraga columbiana*); nutcrackers often place seeds near nurse objects or in protected microsites (Tomback 1982). The pines have similarities and differences in their ecology and physiology (**Table 1**) that impact their distribution and potential response to climate change. Limber pine is considered an ecological ‘generalist’ and whitebark pine a ‘specialist’ (Ulrich et al. 2023).

Questions

Given their physiological similarities and differences, do whitebark and limber pine differ in their frequency of occurrence in functional roles in treeline communities? Do differences in functional roles have climate change implications?

Study Area and Methods

Whitebark pine. Research conducted from 2006 to 2019 across 10 study areas in the northern Rocky Mountains from Wyoming, USA, 42°35’35” lat. N, 108°58’24” long. W, to the northern limits, Alberta, Canada, 53°46’0”, 119°44’22” (**Fig. 3**). Elevation ranged from 3200-3400 m in the south to 1964-2175 m in the north (Tomback et al. 2016a). In 7 study areas, random points used to locate study quadrats; quadrats non-random in 3 study areas with limited access. Quadrats ranged from 225 m^2 to 500 m^2 ; total area sampled ranged from 750 m^2 to 6,750 m^2 per study area.

Limber pine. Research conducted from 2019 to 2021 in Rocky Mountain National Park, 40°20’ 35” lat. N, 105° 41’ 17” long. W, Colorado Front Range, USA (**Fig. 3**). Using GIS and fixed rules, 10 east slope study sites and 9 west slope study sites were selected, ranging in elevation from 3263 to 3622 m (Sindewald (2023). In total 37 quadrats were established, each ~25 x 25 m (625 m^2).

In all study areas and sites, relevant data collected on quadrats included: Prevailing wind direction and all conifers by species and functional roles (including cotyledon seedlings),

For whitebark, we calculated overall proportions of each ATE functional role represented in each study area. We performed linear regression to determine if the proportion of solitary trees that were whitebark pine predicted the proportion of tree island initiators that were whitebark pine. For limber pine, we calculated 95% confidence intervals for mean proportions and performed odds ratio tests to determine whether the proportion of limber pine solitary trees predicted the proportion of tree island initiators that were limber pine.

Tree island functional components

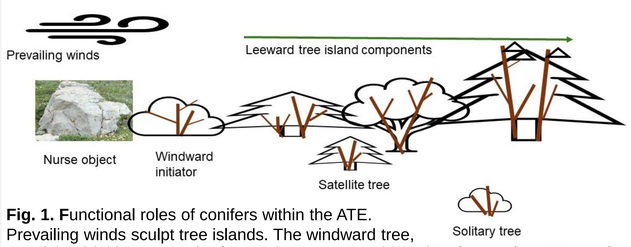

Fig. 1. Functional roles of conifers within the ATE. Prevailing winds sculpt tree islands. The windward tree, *tree island initiator*, may be leeward to a nurse object (Resler et al. 2005, Resler 2006). Trees with overlapping canopies are *tree island components.* Single trees growing farther than tree island height are *solitary trees.* Trees with non-overlapping canopies close to tree islands are *satellite trees.*

Fig. 2. ‘Five-needle’ white pine treeline communities in the Rocky Mountains: (a, b) Limber pine (*Pinus flexilis*) in 2 study sites in Rocky Mountain National Park, CO, USA; (c) whitebark pine (*P. albicaulis*) in a site in the northern Rocky Mountains.

Table 1. Key ecological/physiological similarities and differences between limber pine (LP) and whitebark pine (WP).

Similarities	Differences
Timberline and treeline communities	LP ranges from lower to upper treeline
Seeds are large and wingless	LP cones open; WP cones indehiscent
Directed seed dispersal by Clark’s nutcrackers	LP seeds also dispersed by rodents
Seedlings intolerant of deep snowpack	LP seedlings have higher stomatal density & area
Seedlings require adequate moisture	LP seedlings have higher light tolerance
Trees are slow-growing, late maturing	LP seedlings have higher carbon assimilation rate
At treeline, wind-sculpted and dwarfed	WP forms krummholz mats; LP does not
Treeline stems may produce cones & viable seeds	WP layers (branches root); LP does not
Trees comparatively drought tolerant	LP more drought-tolerant
Prefer well-drained, nutrient poor soils	
Seedlings have similar cold and heat tolerances	
Seedlings have similar photosynthetic capacity	

References: Arno and Hoff 1990, McCaughey and Tomback 2001, Tomback et al. 2016a, Sindewald et al. 2020, Ulrich et al. 2023

Results

Whitebark pine ATE conifer associates included subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), lodgepole pine (*P. contorta), alpine larch (Larix lyallii),* and limber pine. Limber pine associates included subalpine fir, Engelmann spruce, and lodgepole pine.

Among solitary trees, whitebark pine was the majority species in 9 study areas (**Fig. 4a**). One or more whitebark pine occurred across the highest proportion of tree islands of any conifer species except at PR and GP (**Fig. 4b**). Whitebark pine was the most frequently occurring windward conifer and the majority tree island initiator for 5 study areas (**Fig. 4c**). The proportional abundance of whitebark pine among solitary trees predicted its proportional abundance as a tree island initiator (F = 8.724, r = 0.722, df = 8, P = 0.018).

East of the Divide, limber pine occupied the solitary role significantly more often than subalpine fir (difference in proportions = 0.33, 95% CI = 0.18-0.49) and lodgepole pine (difference in proportions = 0.47, 95% CI = 0.38-0.56) but nearly at the same rate as Engelmann spruce (difference in proportions = 0.07, 95% CI = 0-0.20). Limber pine was also found in the satellite role more often than other species, although this difference was not significant (Figure 2.4B). There was no difference among limber pine, spruce, and fir in the odds of any species being in the initiato3 functional role.

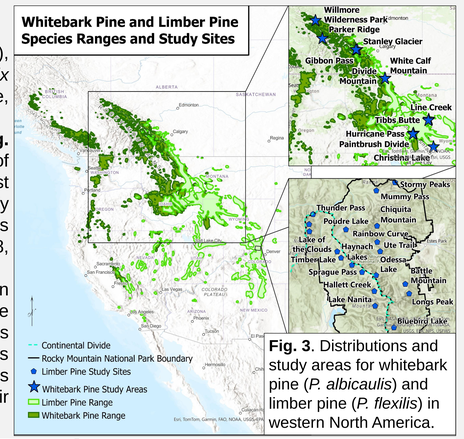

Fig. 3. Distributions and study areas for whitebark pine (*P. albicaulis*) and limber pine (*P. flexilis*) in western North America.

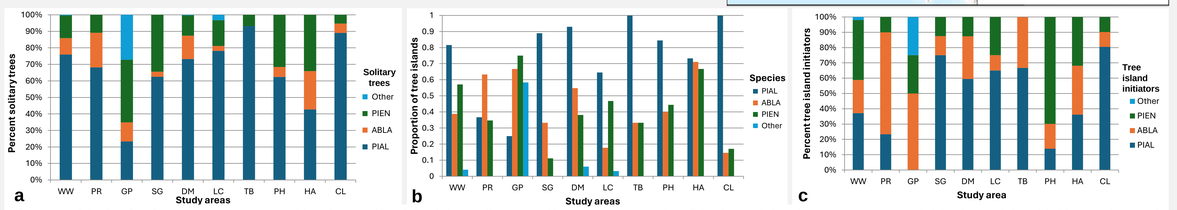

Fig. 4. Whitebark pine: Percent composition by conifer (a) of the solitary conifer tree community, (b) of tree island components, and (c) of tree island initiators for each study area. PIAL= whitebark pine, ABLA = subalpine fir, PIEN = Engelmann spruce, Other = minor conifers. See Fig. 3 for study site names.

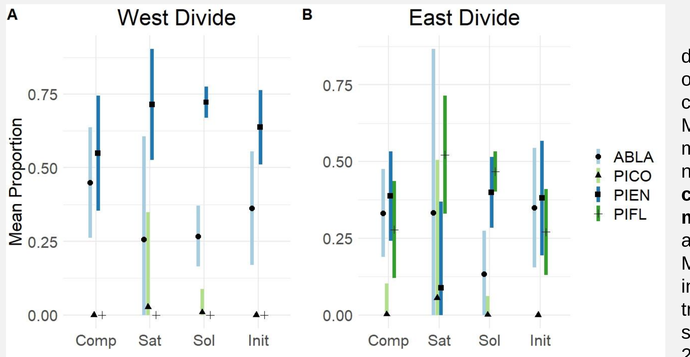

Fig. 5. Limber pine: Proportion of different functional roles filled by conifer species across all quadrats west and east of the Continental Divide (CD). No limber pine occurs west of the CD. Each center point indicates the proportion of each species found in each role. The error bars show 95% confidence intervals for these proportions. Species shown include subalpine fir (ABLA), lodgepole pine (PICO), Engelmann spruce (PIEN), and limber pine (PIFL). Roles include island component (Comp), satellite (Sat), solitary (Sol), and tree island initiator (Init).

Discussion

Whitebark and limber pine assume similar and different functional roles in the ATE. Both commonly occur as solitary trees in the ATE, surviving harsh conditions with little protection (e.g., Germino et al. 1999, McIntire et al. 2016). Their dispersion across the ATE may result from directed seed caching by Clark’s nutcrackers and tolerance of arid conditions. **With climate change, solitary tree establishment may move upwards.** Limber pine is highly drought tolerant, and limber pine trees dominate 4 study sites in Rocky Mountain National Park. Tree island formation is likely initiated by solitary trees and a long process of leeward tree establishment. Whitebark pine appears to be better suited to facilitate this process (Resler and Tomback 2008, Tomback et al. 2016). Whitebark pine assumes the role of tree island initiator frequently, and previous work suggests that whitebark pine canopies offer protection to leeward conifers (Tomback et al. 2016b). **Whitebark is likely to lead treeline response to climate warming in the northern Rocky Mountains.**