Alpine Treeline of Western North America: Linking Organism-to-Landscape Dynamics


Abstract
Although the ecological dynamics of the alpine treeline ecotone are influenced by climate, it is an imperfect indicator of climate change. Mechanistic processes that shape the ecotone – seed rain, seed germination, seedling establishment and subsequent tree growth form, or, conversely tree dieback – depend on microsite patterns. Growth forms affect wind and snow, and so develop positive and negative feedback loops that create these microsites. As a result, complex landscape patterns are generated at multiple spatial scales. Although these mechanistic processes are fundamentally the same for all forest-tundra ecotones across western North America, factors such as prior climate, underlying geology and geomorphology, and genetic constraints of dominant tree species lead to geographic differences in the responses of particular ecotones to climate change.

Keywords: climate change, ecotone, establishment, geomorphology, landscape, scale
Introduction

The transition from subalpine forest to alpine tundra is one of the most distinctive features of mountain environments. Though often referred to as alpine treeline (which we will do here), this ecotone is a zone rather than a line; it varies in all three spatial dimensions between continuous forest at lower elevations and alpine tundra at upper elevations. At a continental scale, the elevation of treeline indicates that it is controlled by temperature, with a decline in elevation at more northerly latitudes and in proximity to coastal locations with maritime climates (e.g., Daubenmire 1954). Change in the elevation of treeline is an expected outcome of regional climate change, and upslope and downslope movements in response to climate variability during the past 20,000 years have been recorded (e.g., Rochefort et al. 1994, Taylor 1995, Lloyd and Graumlich 1997). Such positional change in treeline has important consequences for the adjacent tundra biome. Genetic diversity, habitat for alpine animals, and overall alpine biodiversity are likely to be reduced, and change in tundra areal extent, coupled with changes in treeline community structure, may affect the water and nutrient budgets of mountain watersheds (e.g., Seastedt et al. 2004). However, treeline is controlled by multiple processes (e.g., Holtmeier 2003), so site-specific responses are likely and a lack of change locally does not necessarily indicate climate stability.

Our purpose here is to examine the processes that link treeline to local and regional controls, and so improve our expectations for their response to climate change. Although the ecological mechanisms that create treeline plant composition, structure and spatial patterns are the same across western North America, the relative importance of processes and responses to the environment varies because the environmental contexts are different. Thus, significant variation
in treeline spatial composition and history can occur within and among different mountain ecosystems even with similar climate change, highlighting the notion that there exist many treelines—not one treeline. In this review, we begin with the individual scale and are interested first in the basic biology of tree seedling establishment and, second, in the subsequent development of growth forms (Figure 1, top to bottom). The establishment of new individual seedlings has such a fundamental potential impact on spatial change at treeline that it should be central to the study of its dynamics (e.g., Smith et al. 2003, Daniels and Veblen 2004). We then look at patch-scale dynamics, which reflect interaction among individuals, and finally we examine the landscape scale.

**Individual or local scale mechanisms**

At the scale of individual plants, the mechanisms controlling establishment are largely the same biological processes across western North America. The basic environmental factors of climate, energy and water, directly affect these processes, but the outcomes may differ locally due to abiotic differences and biogeographical history. Climate change may affect successful dispersal, germination and survival by modifying such abiotic conditions as soil availability, quality, and moisture; precipitation fraction arriving as snow; snow redistribution and melt; extent of glacial forefields; extent of permanent snowfields; and disturbance regimes.

*Seeds and germination*

Seed production and dispersal vary among conifers (Family Pinaceae), which typically produce moderate to abundant seed crops every 1 to 4 years (e.g., Young and Young 1992). Because individuals in the ecotone usually produce little seed, dispersal from lower elevations is
necessary (Tranquillini 1979). The winged seeds of most treeline conifers are dispersed by the wind and depend on the proximity and location of seed sources with respect to regional prevailing winds (e.g., Tomback et al. 1990) and surface roughness patterns. In contrast, the few large-seeded, treeline pines depend on birds for seed dispersal (Box 1 [at end])

The second step in potential spatial change of the treeline is seed germination. Germination follows snowmelt and may be most likely in moist microsites at treelines, such as areas with relatively late-lying snow, (e.g., Mellmann-Brown 2005, Resler et al. 2005, Maher and Germino 2006). Butler et al. (2004) associated seedling presence with micro-scale erosion and deposition of fine-grained sediment (likely due to increased penetrability) associated with relict solifluction, a freeze-thaw process that produces patterns such as stripes of coarse and finer substrate (Figure 2). Differences in substrate texture can thus affect the overall pattern of seedling occurrence. Few data, however, are available describing seed abundance, longevity of seeds and seed banks in the soil, or rates of germination success in treeline environments.

*Seedling Survival*

Many treelines in North America occur on exposed, high-elevation slopes, with strong and persistent winds. During winter wind damages the leaders, branches, buds, and leaves of trees and seedlings; however, many trees and krummholz in treelines obviously survive this damage. Seedling survival is extremely low (<10%) in the first year (Smith et al. 2003), but can increase to >90% within the second or third year (e.g., Germino et al. 2002). Burial beneath snow in winter and reductions in sunlight exposure, low temperatures, water stress, and wind are critical environmental factors influencing new seedling survival in summer, along with adaptive
structural attributes for avoiding the severe abiotic environment. Mechanistically, reduction of sky exposure in summer, which lessens night-time cooling and exposure to excessive sunlight, resulted in more favorable microsites and photosynthesis in fir (Abies lasiocarpa) (Germino and Smith 1999), which also orient their needles to minimize sky exposure (Smith et al. 2003). Seedling mortality is often attributed directly to a lack of carbon gain, corresponding root growth, and ensuing desiccation in less favorable microsites (e.g., Hasselquist et al. 2005, Johnson and Smith 2006, Maher et al. 2006). Favorable conditions must persist for several years (e.g., Taylor 1995, Hessl and Baker 1997).

Survival of new seedlings often requires facilitation by microtopographic features, mostly boulders or other plants, that enhance snow burial and reduce abrasion or damage by rime ice, reduce sky exposure, and provide longer-lasting summer soil moisture (Germino et al. 2002, Resler et al. 2005). Even small changes in microtopography such as solifluction, can provide increased snow coverage and seedling protection during winter, as well as protection from sky exposure during summer.

Biotic interactions also affect seedling survival. Tree seedling competition with alpine tundra species may be important (Malanson and Butler 1994), but only if the latter are dense; at lower densities tundra plants can facilitate tree seedling survival (Maher et al. 2005). Predation or trampling by vertebrates occurs in treelines, but to a varying degree (e.g., Mellmann-Brown 2002). Burrowing and digging by mammals of all sizes may create fine-grained sites that are amenable for seedling establishment and survival, but may also expose the excavated sediment to
wind erosion (Butler 1995). Also, the establishment of all conifers in treelines depends on mutualistic root colonization by mycorrhizal fungi (e.g., Cazares et al. 2005).

**Patch scale**

*Growth Forms and Ecological Interactions*

The 3-D pattern at treeline is often patchy, including krummholz (prostrate, laterally growing conifers) and dwarf trees (e.g., Weisberg and Baker 1995, Allen and Walsh 1996). Growth and expansion beyond the initial microsite can be facilitated by other plants (Hattenschwiller and Smith 1999, Resler 2006). Here, the individual directly shapes the patch scale and even species-specific tendencies can be critical for patch development. The formation of vegetation structures that add wind protection, snow collection, and soil development at the spatial scales of a tree island allows newly established subalpine forest species to initiate patches and then to have patches expand and become denser in the upper treeline (e.g., Smith et al. 2003). These structures can also affect the infilling of openings in the tree cover lower in the treeline. In addition to patches per se, often, a linear configuration of trees develops with older individuals closest to the initial, facilitating structure (Holtmeier 1982, Alftine and Malanson 2004, Resler 2006) (Figure 3).

The effect of a patch on its surroundings may be a positive feedback (Malanson 1997, Callaway et al. ????). Once a tree becomes established in a suitable microsite, the growing tree reinforces wind protection and increases snow accumulation and the fine mineral and organic fractions of the soil. This process involves the capability of conifer treeline species to survive as an array of growth forms that include stunted and flagged trees, tree islands, and dense krummholz mats
(Figure 4). These growth forms represent a morphological gradient of structural characteristics across the ecotone that enhance snow collection and burial (e.g., krummholz mats) or respond to and further avoid blowing snow abrasion (e.g., flagging) in drier, colder treeline sites (e.g., Smith et al. 2003). The effects of micro- and meso-topography can counteract the presumed effects of elevation and create counter gradients of these forms. The krummholz shape reduces sky exposure for nearby seedlings as well as providing protection from wind, as indicated by the emergence of vertical stems to form flagged trees on the leeward sides of larger krummholz mats (Figure 4) (Smith et al. 2003). Plants also influence soil formation by adding organic material, changing texture, and increasing soil penetrability (Pérez 1995).

The development of patches also initiates negative feedbacks on seedling establishment. The formation of dense canopies of tree islands adversely affects regeneration within them by shading, decreasing temperature (especially of soil), and accumulating slowly decomposing litter above the mineral soil. Thus dieback is observed at the windward end of migrating tree islands (Benedict 1984). At the patch scale there is also evidence for reductions in tree species cover; recent diebacks have thinned some patches in the Sierra Nevada during extended droughts (e.g., Millar et al. 2007). More generally, feedbacks and climate conditions must be harsh enough to overwhelm any positive feedbacks for mature individuals. Furthermore, changes in patches influence neighboring patches and create landscape patterns.

**Landscape scale**

*Constraints on pattern and process*
The constraints that control the dynamics of treelines are the climate at regional scale and landscape scale variation in geomorphology or geology. Studies of the relationship between disturbance and the treeline have emphasized the constraining character of geomorphic processes and structural and lithologic controls (e.g., Butler and Walsh 1994). The freeze-thaw cycle in the periglacial climate of treeline leads to geomorphologic processes include solifluction, soil creep, landslides, and erosion by wind and water at this scale. Snow avalanches and debris flows can cause tree mortality and limit treeline elevation through disturbance (Butler and Walsh 1994). At a yet coarser scale, the expansion of krummholz or tree-island patches on a landscape may be limited by topographic constraints, such as cliffs, and the ecotone pattern encounters a stable boundary.

*Patch dynamics at landscape scale*

In alpine systems redistribution of snow by wind is a defining feature of the physical environment. In these landscapes, snow, wind, and topography interact with vegetation to produce a pattern of snow deposition: snow is eroded by wind from exposed areas and deposited on the lee sides of hills, trees, and rocks (Figure 5)(Walsh et al. 1994, Hiemstra et al., 2006), creating strong gradients in the distribution of snow. Snow cover at treeline produces both facilitative and inhibitory effects. Snow can protect seedlings and stems in winter from damage by low temperatures and physiological aridity and abrasion due to wind, affect winter soil temperatures, and provide soil moisture through melting in spring and summer; however snow may also limit the growing season and create avalanches as frequent disturbances.
The effect of established krummholz or trees, plus topography, determine how wind and snow alter the pattern and dynamics of habitat across and among slopes, within which trees species can successfully establish in the ecotone. Specifically, facilitation is unimodal, wherein too few or too many neighboring trees reduce the potential for new establishment. Treeline dynamics change when a patch expands to the point where the positive feedback becomes limited by negative feedback. Using a simple, two-state tree-versus-tundra model, Zeng and Malanson (2006) showed that a wide range of patterns exist at simulated treelines, which fluctuate fractally. They explained that establishment of individuals accelerated the advance of treeline, as positive feedback affected a wide number of possible establishment sites. This change led to a coalescence of patches that decreased the number of establishment sites in the vicinity of the trees, which slowed advance.

Coarse-scale constraints limit further landscape development. Geologic control, where forest is terminated by cliffs is primary. Second is lithologic control, where weathering produces variability in the texture and chemistry of the substrate. Third, snow and debris avalanches greatly lower mapped treelines locally. Next, differences in topography, from the steeply concave U-shaped valleys to the broader convex interfluves, change the breadth of the ecotone. Finally, the particular species composition creates patchy and fingering krummholz and/or dwarf tree islands. Thus local topography and biogeography modify the mesoscale inputs of energy and water (Box 2 [at end])

Conclusions
Alpine treelines have long been considered visual barometers of change in topography where environmental gradients are sharp, and the vegetation patterns are apparent. They have captured the imagination of a broad sector of the public, because many people greatly value high-elevation locations. People see in the wind-flagged, contorted trees the epic struggle of nature against the elements. There is a very real cultural identity associated with the geology, plants, and animals that characterize subalpine and alpine ecosystems – these systems have come to symbolize pristine mountain environments.

As such, treelines simultaneously reflect biological responses and human values, making these ecotones an important focus for management, scientific study, and assessment of ecosystem services. Recent studies of treelines have explored the potential for these locations to record and manifest the effects of climatic variability and change--a possible “canary in the mine” that may portend more extensive ecological changes in mountain ecosystems of western North America. The change clearly will not, however, be a simple upward movement of a line.

While all treelines in western North America share the same sets of mechanisms leading to establishment, landscape responses to climate change are idiosyncratic, based on specific combinations of geology, geomorphology, and climate trends. Yet feedbacks and time-lags in system behavior mean that vegetation and climate are only loosely coupled, and geology and geomorphology may be more important than previously thought. Moreover, given that climate change is not linear, response or lack thereof in any decade or two may not clearly illustrate cause and effect.
Finally, advance of trees into tundra can change high-elevation montane ecosystem services, such as carbon, water, and nutrient cycles, feedbacks to the climate system, and maintenance of biodiversity. Tree establishment at some locations has increased carbon storage through accretion of living vegetation. Transfer of this carbon to dead biomass and soil organic matter results in a long-term carbon sink under cool, wet conditions and/or with less frequent fire in this sparse fuel environment. Advance of trees, or change in pattern in general, also has the potential for altering snow retention and hydrology, with implications for local, soil moisture, and nutrient transport, given how pattern directly affects wind and thus aeolian erosion and deposition of snow and sediment, which indirectly affects soil temperatures and runoff (Seastedt 2004). Changes in albedo and surface roughness are other feedbacks to the climate system, although of lesser impact. Potentially of most importance, habitat for alpine animals and biodiversity in the tundra are likely to be affected by changes in treeline landscapes.

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Figure captions

Figure 1. An environmental sieve indicating the main sequence of processes by which establishment at the alpine forest-tundra ecotone may be limited.

Figure 2. Micro-erosion of solifluction risers onto the treads provides an exposed soil seedbed for germination and establishment; Glacier National Park, MT.

Figure 3. Advance of tree species into tundra is often patchy, including linear forms parallel to the prevailing wind, Lee Ridge, Glacier National Park, MT.

Figure 4. Patches of krummholz develop into trees islands at their leeward extent; Medicine Bow Mountains, WY.

Figure 5. Late lying snow in the lee of tree islands at Libby Flats, Medicine Bow Mountains, WY.

Figure 6. A hedge of krummholz and dwarf trees develops downwind of a small boulder; Glacier National Park, MT.

Figure 7. Blister rust (*Cronartium ribicola*) on a branch of whitebark pine (*Pinus albicaulis*) at a treeline site, Glacier National Park, MT.
Figure 8. Coarse granitic substrate supports patches of small upright foxtail pine (Pinus balfouriana), Inyo National Forest, CA.

Figure 9. Large solifluction forms develop where the coarse granitic substrate is supplemented by the input of fine aeolian sediments in the southern Rocky Mountains, Niwot Ridge LTER, CO.
In a nutshell

- Seedling establishment at alpine treeline requires a specific combination of biological, climatic and geomorphic conditions, which may result from processes that themselves are responses to climate change.

- Patches of krummholz or dwarf trees develop because positive feedbacks improve conditions for establishment and growth in the immediate neighborhood of extant plants, but are eventually limited by negative feedbacks.

- Patches form, grow, and coalesce locally – altering the pace of establishment and growth across hillslopes or landscapes – so patterns change through time.

- Treeline patterns and processes differ due to regional geology, geomorphology, and climate history, so responses to climate change are locally individualistic.
Keystone species?

Whitebark pine (*Pinus albicaulis*) plays a special role within the alpine treeline community; it is known to serve as a foundation and keystone species in subalpine communities (e.g., Tomback 2001). Its large, wingless seeds depend on the seed dispersal services of Clark’s nutcracker (*Nucifraga columbiana*, Family Corvidae), a bird whose seed caches are often in protected microsites (e.g., Tomback 2001) and thus become spatial hotspots for regeneration. Whitebark pine is a hardy pioneer, with unusually robust, stress-tolerant seedlings (Tomback 1986, Tomback et al. 2001, Mellmann-Brown 2002, 2005). At the eastern front of the northern continental divide of the Rocky Mountains, whitebark pine is often the first conifer species to establish in a safe microsite within the treeline community or in tundra, The pine also serves as a facilitator for establishment and growth of spruce and fir in its immediate lee (Figure 6)(e.g., Resler 2006). Both whitebark pine and its relative limber pine (*Pinus flexilis*), a large-seeded, nutcracker-dispersed pine which occurs at treeline in the central Rocky Mountains, are known to facilitate the establishment of less hardy forest associates on harsh sites within the subalpine forest communities (e.g., Rebertus et al. 1991).

The introduced fungal pathogen *Cronartium ribicola*, which causes white pine blister rust, has spread throughout most of the collective ranges of five-needled white pines in North America (McDonald and Hoff 2001). In some heavily infected areas, including the northern Rocky Mountains of the USA, blister rust is damaging and killing krummholz whitebark pine trees (Figure 7; Tomback, Resler and Daniels, unpublished observations). Furthermore, as seed
production diminishes in subalpine forests from the spread and intensification of blister rust, fewer seeds will be dispersed to treeline elevations. Thus blister rust has the potential to alter the composition and dynamics of treeline communities throughout much of western North America by eliminating five-needled white pines.
Regional contrasts

At regional scales we see commonalities and differences in the constraints on the finer scale processes.

Climate

Maritime climates lack summer warmth and receive much more snow, which is denser and less mobile, than continental climates. Growing seasons are abbreviated compared with continental climates at the same latitude. Thus the Pacific Northwest will differ from interior regions because it is strongly maritime. Longer lasting snowpack could limit any expansion of patches of krummholz higher in the ecotone and could expand lower meadows. This effect is dependent on increasing precipitation in the form of snow, which may not be the case. Even in small areas, e.g., within Glacier National Park, MT, we do see, however, a contrast in patterns between the maritime western slopes and the strongly continental slopes east of the continental divide, where there are more patches of krummholz within the tundra matrix. Here and elsewhere in the West areas are drier, so increasing moisture will likely improve the conditions for tree species establishment and growth. The effect is likely to be greatest lower in the ecotone where deeper soils and root zones can more readily take advantage of the increased water. The effect will possibly be greatest in the southern Rocky Mountains and least in the Sierra Nevada, because of differences in substrate development and water-holding capacity, assuming equivalent climate changes. Millar et al. (2004) and Bunn et al. (2005b) reported increased tree-ring widths at Sierra Nevada treelines for warmer, wetter periods in the 20th century. Millar et al. (2004) also found
increasing invasion of subalpine meadows during drier periods – the elevational switch that we would expect, because deep snow in lower elevation meadows limits establishment even in more continental sites (e.g., Moir et al. 1999).

Altered productivity of alpine tundra is another consideration. Malanson and Butler (1994) conjectured that competition from denser tundra, due to differences in nutrients, could limit the establishment of tree species and affect upper treeline elevation. Conditions of shorter snow durations in the Pacific Northwest or warmer and wetter climate elsewhere could favor an increased density of tundra or meadow plants and slow the spatial response of subalpine forest.

**Geology and Geomorphology**

Glacial erosion has created glacial topography across western North America, but other geological features have more important influence on the elevation of treeline. Substrate texture varies strongly geographically, with the coarsest developed on the Mesozoic granite batholith in the Sierra Nevada (Figure 8), which contrasts with the coarse fellfields of Precambrian gneiss, schist and granite mixed with aeolian deposition of fine sediments in the Colorado Rockies (Figure 9). Further contrasts can be seen within the Sierra where fir dominates on other substrates and creates different forms with krummholz patches (e.g., Millar et al. 2004), and in the White Mountains, CA, where bristlecone pine is primarily confined to dolomite at treeline (e.g., Wright and Mooney 1965).

Perhaps due to the aeolian inputs, solifluction forms are large in the southern Rockies but also prevalent further north (Figure 8). Wetter conditions or more freeze-thaw cycles could increase
solifluction activity and forms, which may improve the substrate for seedling establishment
(Butler et al. 2004, Resler et al. 2005).

**Biogeography**

Despite general regional similarities in conifer associations, some differences are also evident, such as the high elevation open stands of large, upright growth forms of foxtail pine (*Pinus balfouriana*) in the Sierra Nevada (Figure 8) or the picturesque shapes of bristlecone pine (*Pinus longaeva*) in the western Great Basin. Elsewhere, *Pinus albicaulis* plays a potentially critical role in the process of patch formation at treeline (Box 1). These and other high elevation five-needled white pines show idiosyncratic responses to harsh environments, and contribute both to the structural diversity and the biodiversity of western treeline communities.