

## Fire enhances the complexity of forest structure in alpine treeline ecotones

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**Abstract.** Alpine treelines are expected to move upward in a warming climate, but downward in response to increases in wildfire. We studied the effects of fire on vegetation structure and composition across four alpine treeline ecotones extending from *Abies lasiocarpa*/*Picea engelmannii* forests at lower elevations, through *Pinus albicaulis*/*Larix lyallii* parkland, to alpine tundra. We estimated the probabilities of burning and transitions between states following fire among four canopy-cover (structural) classes: non-forest (0% tree cover), sparse woodland (<10% tree cover), open forest (10–40% tree cover), and closed forest (>40% tree cover). We also evaluated changes in the size structure and composition of live overstory trees ( $\geq 1.4$  m height) due to mortality following fire. The severity and resulting effects of fire varied among structural classes: Non-forest was less likely to burn than the landscape as a whole; open forest was more likely to remain forest than to change to non-forest; and closed forest never changed to non-forest, irrespective of burn severity. Higher-severity fires caused greater mortality of larger-diameter trees than of smaller-diameter trees. Our results suggest that structural components of the alpine treeline will not respond unidirectionally to a warming climate nor to an increase in fire. Instead, the ecotone will expand bidirectionally and develop larger, more heterogeneous patches of vegetation.

**Key words:** *Abies lasiocarpa*; *Larix lyallii*; North Cascades; Northern Rockies; Pacific Northwest; *Pinus albicaulis*;

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### INTRODUCTION

The influences of climate and local feedback on tree establishment and growth in the alpine tree-line ecotone (ATE)—the transitional area spanning the upper edge of closed forest to treeless alpine—have been studied extensively (Körner 2012). Multiple lines of evidence indicate that upright tree growth in the ATE relates strongly to climate. These include (1) observational studies of vegetation distribution (Daubenmire 1954), (2) relationships between climate and treeline fluctuations during the Holocene (Rochefort et al. 1994, Lloyd 2005), (3) correlations between tree growth (ring width) and climatic variables (Paulsen et al.

2000, Peterson 2002, Ettinger et al. 2011), and (4) the strong influence of microtopography and neighboring vegetation on tree establishment and survival (Callaway et al. 2002, Malanson et al. 2011). A warming climate is expected to favor tree establishment in the ATE and an upward movement of treeline (Malanson et al. 2011). Recent observations suggest that these changes have begun in some ecosystems (Danby and Hik 2007, Harsch et al. 2009).

In western North America, climate warming has also contributed to increased area of wildfires (Littell et al. 2009, Wotton et al. 2010, Abatzoglou and Williams 2016) and in some places to increased severity and size of high-severity

patches within these fires (Cansler and McKenzie 2014). Further increases in area burned are expected under climate change (Flannigan et al. 2009, Littell et al. 2010). The conditions likely to enhance tree establishment in the ATE—decreased snowpack and longer growing seasons—are also conducive to greater probability of wildfire. Our analysis of recent (1984–2012) wildfires in eight ecoregions of the Pacific Northwest and Northern Rocky Mountains indicates strong correlations between total area burned and area burned in both subalpine vegetation and alpine vegetation (Cansler et al. 2016). In fact, in four regions, subalpine parkland burned more, on a proportional basis, than did the landscape as a whole. Across the combined set of ecoregions, 7% of subalpine parkland burned vs. 8% of the broader landscape. Conversely, <3% of alpine (non-forested) vegetation burned (Cansler et al. 2016). Thus, the assumption that fire is uncommon or unimportant in the ATE (Malanson et al. 2011) may not hold in a modern warming climate (Higuera et al. 2014, 2015), or it may apply only to non-forested meadows, fell fields, and tundra.

Because tree establishment proceeds slowly in the ATE, disturbance and past climate can have persistent influences on vegetation. Disturbances may originate from human activities (e.g., firewood gathering, grazing, or intentional burning) that create “anthropogenic treelines” (as described by Holtmeier and Broll 2005) or from “natural” causes (e.g., insects, fire, or severe climate events). Moreover, evidence of past disturbance may no longer be present (Malanson et al. 2011). For example, historical grazing, mining, and anthropogenic burning have maintained treeline in the European Alps at an average of 150–300 m below climatic limits (Malanson et al. 2011). Similarly, fires of natural or anthropogenic origin likely limited the upward movement of tropical treelines during much of the Holocene (Bader et al. 2007, Di Pasquale et al. 2008). In fact, in some regions, such as the European Alps, the history of human disturbance may be the primary determinant of current treeline (Holtmeier and Broll 2007).

Despite the abundance of research on climatic controls and the acknowledged importance of site history in the ATE of Europe, little research has addressed the influence of disturbance on

the ATE of western North America (Whitesides and Butler 2010, Malanson et al. 2011). The few relevant studies suggest that even if wildfires are small (or uncommon) in the ATE, their effects are more persistent than at lower elevations. For example, on the western slope of the Cascade Range, regeneration of trees was minimal three decades after fire (Douglas and Ballard 1971), and in the Olympic Mountains, it did not peak until 40–70 yr after fire (Agee and Smith 1984). In continental climates, post-fire regeneration appears more rapid (peaking after 17–25 yr; Tomback et al. 1993), possibly reflecting the longer growing season or prevalence of early-seral (open site) pine species. In contrast, in the drier central Rocky Mountains, abiotic stress (Billings 1969) or competition from herbaceous species (Stahelin 1943) can inhibit post-fire regeneration of trees, thus shifting dominance to forbs or graminoids.

It is unclear how the direct and indirect effects of a warming climate and associated changes in fire regime will affect the distribution and structure of vegetation in the ATE (Fig. 1). Recent increases in area burned (Cansler et al. 2016) could maintain or expand areas of non-forested vegetation. Alternatively, by removing competing vegetation, fires could facilitate tree regeneration, hastening responses to climate change, as observed at some latitudinal treelines (Brown 2010). Fire could also alter tree spatial distributions (Baker and Weisberg 1995), size structure, or composition, if mortality varies spatially, or is size- or species-dependent. For example, smaller trees (including krummholz) may be more susceptible to fire because their branches and buds are closer to surface fuels. Among larger (mature) trees, interspecific differences in bark thickness or canopy architecture may contribute to greater fire tolerance in *Pinus albicaulis* (Arno 1980, Larson and Kipfmüller 2010) than in associated alpine species. Likewise, the dependence of *Larix lyallii* on fire refugia (cool, wet, or rocky areas within the ATE) may indicate limited tolerance of fire (Arno and Habeck 1972). As burn area increases, however, these refugia may become increasingly susceptible to fire. Because changes in the distribution and structure of vegetation have implications for many ecosystem services (e.g., wildlife habitat, hydrologic and nutrient cycling, and carbon sequestration),

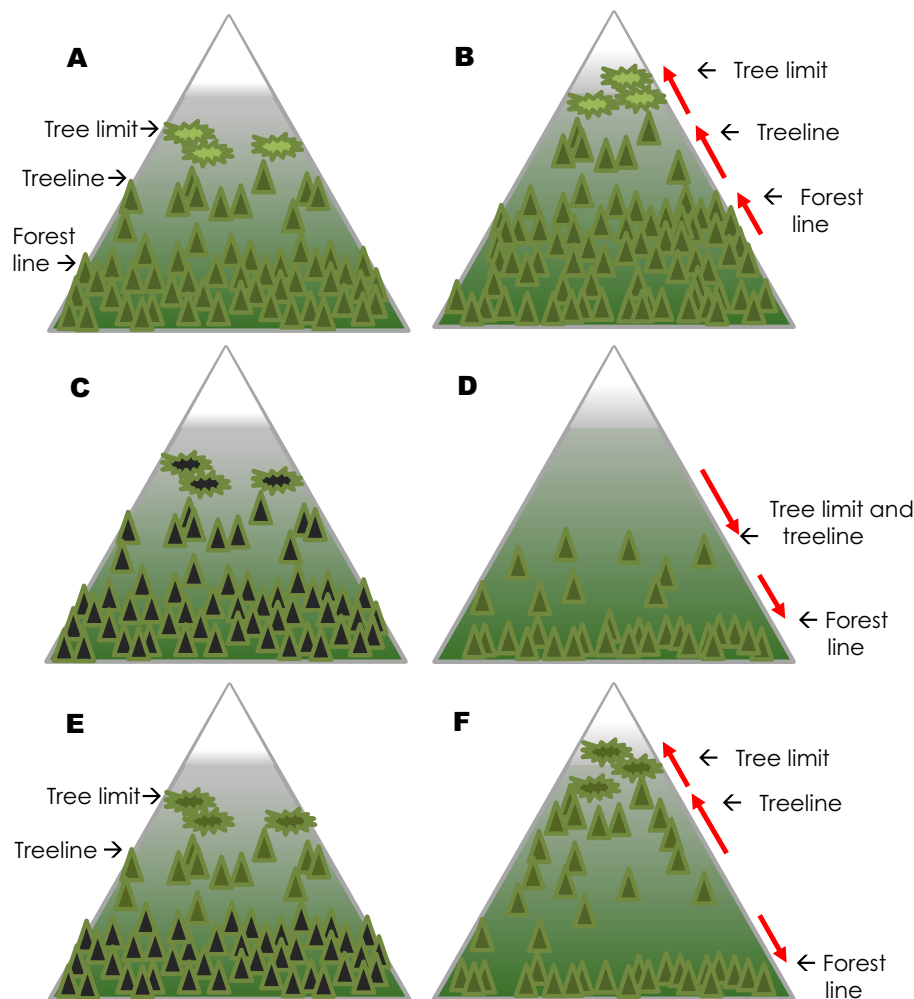


Fig. 1. Conceptual model of vegetation changes in the alpine treeline ecotone (ATE) due to climate warming (top row) and the combined effects of climate warming and fire (bottom two rows). The current condition is represented by A. With climate change, tree limit, treeline, and forest line are expected to rise in elevation (red arrows, B). C represents post-fire conditions if the entire ATE burned. Fire results in a long-term suppression of tree limit, treeline, and the forest line (red arrows, D). Post-fire recovery is slow, but is likely to be faster near the forest line than the tree limit. If fire were to burn only to the forest line (E), with climate warming the upper tree limit would ascend but the lower edge of the ecotone would descend (F). In sum, the change due to climate warming likely differs from that due to fire (increase vs. decrease in tree cover, respectively) resulting in combined effects that differ from those caused by either factor alone.

understanding the effects of fire in the ATE is critical.

In this study, we examined variability in fire severity, tree mortality, and changes in vegetation structure in the ATE 18–27 yr after fires of mixed severity at four locations in the western United States. Our goal was to elucidate how fire—through effects on tree mortality—changes the

distribution, structure, and composition of vegetation within the ATE. We addressed three questions: (1) What are the probabilities of burning at differing severities for each of four principal vegetation types (structural classes): closed forest, open forest, sparse woodland, and non-forest (alpine and meadow)? (2) If a structural class burns, how likely is it to change to a different

structural class? (3) Within forested portions of the ATE, how does fire-induced mortality affect the size structure and composition of trees?

## METHODS

### Study locations

We sampled four high-elevation wildfire sites between July and September 2012 in National Forests in the Pacific Northwest and Northern Rockies, USA (Table 1, Fig. 2). Two were in the northern Cascade Range of Washington state: the Hubbard Creek (1985) and Butte Creek (1994) fires. Two were in the Northern Rockies: the Upper Bear fire (1998) in the Bitterroot Mountains on the Idaho–Montana border and the

Helen Creek fire (1994) in the Bob Marshall Wilderness, Montana. Sites were selected from a larger set of recent wildfires in the Pacific Northwest used in a geospatial analysis of burning in ATEs (Cansler et al. 2016). The four sites for the current study were selected because large areas of the ATE had burned and were reasonably accessible by trails (<2-d hikes). All had burned 18–27 yr earlier, allowing us to assess the effects of mortality from fire and post-fire vegetation recovery (Cansler 2015).

Based on 1981–2010 normals, Helen Creek had the most continental climate with the lowest temperatures and lowest precipitation, whereas Hubbard Creek had the most mesic climate, with higher precipitation and lower climatic-moisture

Table 1. Dates of fires, locations, elevations, dominant tree species, climate normal, and climate in years before, during, and after the fire in the four study sites.

Variables	Hubbard Creek	Butte Creek	Upper Bear	Helen Creek
Year burned	1985	1994	1988	1994
Location	Northern Cascade Range (Washington)	Northern Cascade Range (Washington)	Bitterroot Mountains (Idaho, Montana)	Bob Marshall Wilderness (Montana)
Latitude	47.72	48.35	46.13	48.49
Longitude	–113.24	–120.55	–114.51	–120.51
Elevational range (m)	2150–2460	1850–2255	2050–2390	1850–2400
Elevation mean (m) <sup>†</sup>	2305	2053	2220	2125
Dominant tree species	<i>Abies lasiocarpa</i> , <i>Larix lyallii</i> , <i>Picea engelmannii</i>	<i>A. lasiocarpa</i> , <i>Pinus albicaulis</i> , <i>L. lyallii</i>	<i>A. lasiocarpa</i> , <i>Pin. albicaulis</i> , <i>Pinus contorta</i> subsp. <i>latifolia</i>	<i>A. lasiocarpa</i> , <i>Pin. albicaulis</i> , <i>Pic. engelmannii</i>
Mean annual temperature (°C)				
1981–2010	0.6	1.3	2.4	0.8
Year before fire	<b>1.5</b>	<i>0.6</i>	<b>2.5</b>	<i>0.1</i>
Fire year	–1.2	<b>2.2</b>	<b>3.5</b>	<b>1.6</b>
Mean warmest-month temperature (°C)				
1981–2010	11.7	10.5	13.8	10
Year before fire	<i>10.7</i>	<i>9.1</i>	<b>14</b>	<i>8.6</i>
Fire year	<b>14.3</b>	<b>11.9</b>	<b>14.8</b>	<b>11.5</b>
Mean annual precipitation (mm)				
1981–2010	1613	1558	1672	1342
Year before fire	<i>1506</i>	<i>1196</i>	<b>1852</b>	<i>1043</i>
Fire year	<i>1429</i>	<b>1669</b>	<i>1426</i>	<b>1433</b>
Hargreaves climatic-moisture deficit (mm)				
1981–2010	66	138	142	158
Year before fire	<b>118</b>	<i>64</i>	<b>199</b>	<i>80</i>
Fire year	<b>170</b>	<b>212</b>	<b>222</b>	<b>240</b>

Notes: Climate data are from ClimateNW (Wang et al. 2012), which interpolates climate values based on elevation and latitude from 400-m base data from the Parameter-Elevation Regressions on Independent Slopes model (PRISM) Climate Group (Daly et al. 2008). Bold and italic fonts indicate higher and lower values, respectively, than the 1981–2010 normal.

<sup>†</sup> Elevation used to calculate climate data.



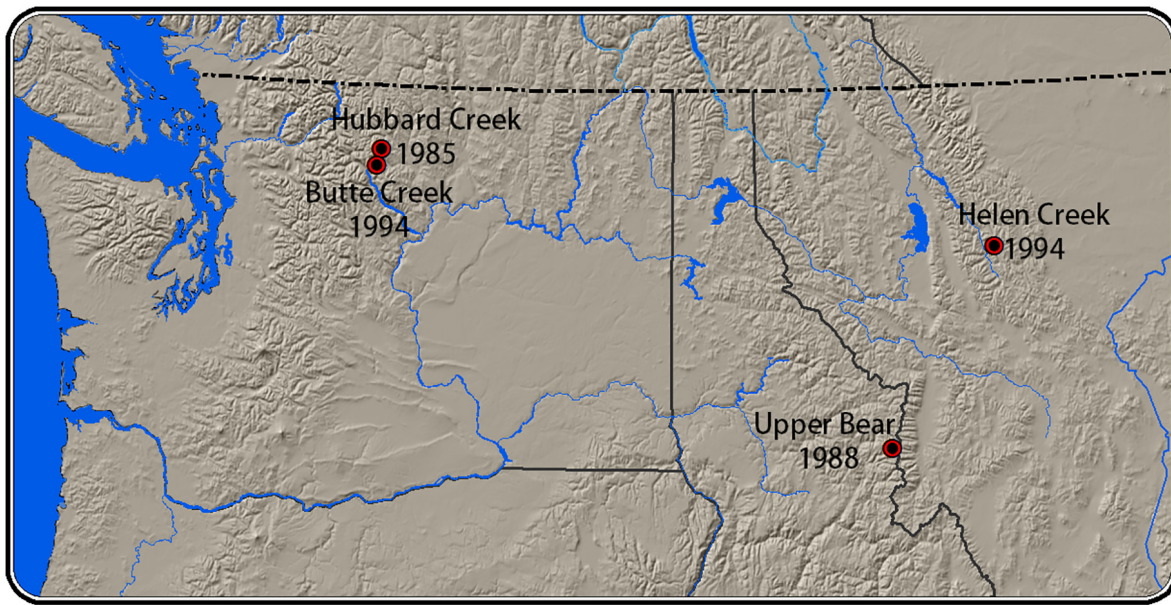


Fig. 2. Locations of study sites and dates of wildfires.

deficit (Table 1). Butte Creek was more mesic than Upper Bear, but had less summer precipitation (Table 1). In fire years, all sites had above-normal warmest-month temperatures and above-normal climatic-moisture deficits. In addition, all sites except Hubbard Creek had below-normal growing-season precipitation. In the years before fire, Hubbard Creek and Upper Bear had above-normal climatic-moisture deficits. Drought in years preceding fire usually increases fire severity due to long-term declines in live and dead fuel moisture. Physiological stress associated with drought can also increase the likelihood of mortality in fire-damaged trees (van Mantgem et al. 2013).

Upper elevational limits included the highest elevations not classified as cliffs, permanent snowfields, talus, or barrens in both the Gap Analysis Land Cover data (National Gap Analysis Program 2011) and the LANDFIRE existing vegetation data (Rollins and Frame 2006). Lower elevational limits were defined as areas of closed forest (>40% tree cover) no more than 150 m below areas of open forest (10–40% tree cover) or sparse woodland (<10% tree cover; see *Methods: Burn-severity and canopy-cover structural classes* for descriptions of vegetation structural classes). Minimum elevations were site specific, derived from photo-interpretation in Google Earth of the typical

upper limit of continuous forest. Thus, sites were bounded at lower elevations by closed *Abies lasiocarpa*/*Picea engelmannii* forests and extended upward through a mosaic of *Pinus albicaulis*/*Larix lyallii* parkland into alpine tundra (see Table 1 for dominant tree species at each site); nomenclature follows the PLANTS National Database (<http://plants.usda.gov>). The structure or “treeline form” of ATEs in this study is of the “diffuse” or “island” form (sensu Harsch and Bader 2011): With increasing elevation and environmental stress, trees decrease in height and occur in clumps or patches. Krummholz tree forms were present, but uncommon, and typically occurred adjacent to upright trees (usually *Pin. albicaulis*).

### Sampling methods

*Gridded and structural plots.*—We used different sampling strategies to address different questions. To characterize the probabilities of pre-fire structural classes burning at differing severities (Question 1), and of changing in class after fire (Question 2), we used “gridded” plots (0.07 ha; 15 m radius circle) to sample the ATE landscape (Table 2). Plots were spaced 150 m apart from a random start and encompassed areas both within and adjacent to (within 300 m of) each fire. To characterize changes in the size structure and

Table 2. Numbers of gridded and structural plots in burned and unburned areas at each site.

Site	Gridded plots		Structural plots	
	Burned	Unburned	Burned	Unburned
Hubbard Creek, Northern Cascade Range	45	10	21	23
Butte Creek, Northern Cascade Range	55	28	42	26
Upper Bear, Northern Rocky Mountains	53	6	24	8
Helen Creek, Northern Rocky Mountains	75	38	48	28

species composition of trees due to fire-induced mortality (Question 3), we used “structural” plots (0.01 ha; 20 × 5 m; Table 2). Here, we used a stratified random approach based on burn history (burned vs. unburned) and vegetation cover-type (forest, sparse woodland, or non-forest). Burned vs. unburned areas were delineated using fire perimeters from classified MTBS images (Monitoring Trends in Burn Severity; Eidenshink et al. 2007). Cover-types were identified from Gap Analysis Land Cover data (National Gap Analysis Program 2011; Appendix S1: Table S1) and confirmed against LANDFIRE existing vegetation data (Rollins and Frame 2006). If a severity class or cover-type did not correspond to our field observation, it was reassigned in the field (see details in *Burn-severity and canopy-cover structural classes*, below). For both gridded and structural plots, we avoided permanent snowfields, unvegetated talus fields, avalanches, standing water, slopes >100%, and sites that were inaccessible or hazardous.

*Burn-severity and canopy-cover structural classes.*—Each gridded or structural plot was assigned to one of four burn-severity classes based on the proportion of trees that died and the abundance

of soil charcoal (Table 3, Fig. 3). Classes followed previous descriptions of burn severity from field studies (Key and Benson 2006), remote sensing analysis (Miller and Thode 2007, Cansler and McKenzie 2012), and characterizations of fire regimes (Agee 1993, Rollins and Frame 2006). Each plot was also assigned to one of four canopy-cover (structural) classes based on a visual estimate of canopy cover (i.e., trees ≥1.4 m tall): non-forest (0% tree cover), sparse woodland (<10% tree cover), open forest (10–40% tree cover), and closed forest (>40% cover; Table 3, Fig. 4). Definitions of forest and woodland vary (Sasaki and Putz 2009); we adopted the cover thresholds of 10% and 40% used in global initiatives on forest, land use, and climate change, such as the Global Forest Resources Assessment (Keenan et al. 2015), the Millennium Ecosystem Assessment (Shvidenko et al. 2005), and the UN Convention on Climate Change (IPCC 2007). These are similar, but not identical, to the thresholds used to delineate sparse vegetation (<10% cover) and closed canopy forest (typically >60% tree cover) in national geospatial land-cover products (Rollins and Frame 2006, National Gap

Table 3. Descriptions of canopy-cover (structural) and burn-severity classes.

Class	Description
<b>Structural class</b>	
Non-forest	No cover of overstory trees (≥1.4 m tall)
Sparse woodland	<10% overstory tree cover; includes plots with only krummholz trees (prostrate trees <2 m tall)
Open forest	10–40% overstory tree cover
Closed forest	40–100% overstory tree cover
<b>Burn-severity class</b>	
Unburned	No evidence of fire
Low	Surface fire; few if any trees killed or only a small portion of area affected; charcoal in the soil or on down woody debris
Moderate	Surface fire with occasional consumption of individual trees; 20–70% of trees killed; charcoal in the soil or on down woody debris
High	Continuous surface fire with torching or fire carried through the crown; 50–100% of trees killed; charcoal in the soil or on down woody debris; post-fire erosion often evident

*Note:* Canopy cover was assessed at different scales for gridded plots (0.07 ha) and structural plots (0.01 ha).





Fig. 3. Examples of burn-severity classes: unburned (top left), low severity (top right), moderate severity (bottom left), high severity (bottom right).

Analysis Program 2011, LANDFIRE Mapping Team 2016).

*Reconstructions of forest structure and composition.*—We reconstructed the immediate post-fire density and size structure of live trees in the structural plots. We recorded the species and diameter at breast height (dbh) of all trees. Trees >5 cm dbh were measured to the nearest 0.1 cm; smaller trees were assigned to one of three dbh classes ( $\leq 1$ , >1–2.5, and >2.5–5 cm). Age reconstructions from branch whorls (as well as growth morphology) indicated that all trees >1.4 m tall had established before fire. Trees that died more recently (those with fine branches or brown needles; Appendix S1: Fig. S1) were included in these reconstructions.

We used the same plots to reconstruct the pre-fire density of trees. Because wood

decomposes slowly in the ATE, we were able to use characteristics of dead trees to determine pre-fire status (live or dead) and identity. First, for all stems on the ground, presence in a plot was based on the center of the bole at its rooting location. Pre-fire status was then determined as follows. Recent snags (with fine branches or brown needles) and burned snags with no evidence of fire in the heartwood were assumed live at the time of fire. In contrast, snags that had burned in the heartwood and downed stems that burned at the tree–soil interface were assumed dead at the time of fire (Appendix S1: Fig. S1). We identified to species 92.5% of trees dying from fire. The rest were assigned to *A. lasiocarpa*, *Pic. engelmannii*, or *Pinus contorta* in proportion to the distributions of live stems of these species among size and canopy-cover classes at each site (dead stems





Fig. 4. Examples of pre-fire canopy-cover (structural) classes as reconstructed in the field. Pre-fire non-forest (top left), sparse woodland (top right), open forest (bottom left), closed forest (bottom right).

of all other species could be identified in the field).

We acknowledge several potential sources of uncertainty in our reconstructions. First, we may have incorrectly identified some dead stems. Second, we may have misclassified pre-fire status. For example, trees that died shortly before fire may have had heartwood with sufficient moisture to prevent charring and thus were recorded as live. Second, although growth is slow in the ATE, we did not account for post-fire diameter growth; thus, we may have overestimated pre-fire diameters. Conversely, we did not account for loss of bark or sapwood in trees killed by fire; thus, we may have underestimated some pre-fire diameters. The magnitude of these errors is likely to be small, however, compared to the changes in density and size structure due to mortality.

### Statistical analyses

*Relationship between canopy-cover class and other measures of structure.*—We first confirmed whether structural classes—inferred from field estimates of canopy cover—differed in their structural characteristics (density and size distribution of trees). Parametric and non-parametric tests yielded significant differences in the total density and size distribution of trees among canopy-cover classes, supporting use of the latter in subsequent analyses (see Appendix S1: *Relationship between canopy-cover classes and other measures of structure*; Tables S2, S3; Figs. S2, S3). Hereafter, we refer to these as structural classes.

*Probability of burning at varying severities (Question 1).*—To quantify the probabilities of structural classes burning at differing severities, we calculated, for each site, the proportions of gridded plots within each structural class that



burned at each level of severity. Structural classes with few plots were excluded (i.e., closed forest at Upper Bear and Helen Creek and non-forest at Butte Creek). Pearson's chi-square tests ( $4 \times 4$  contingency table) were used to test the null hypothesis that severity did not differ among structural classes. For each site, expected values were derived from the proportion of plots within each structural class and the distribution of burn severity over the landscape as a whole (Zar 2010). *P*-values were based on Monte Carlo simulations (Hope 1968, Patefield 1981), and significance was assessed at  $\alpha = 0.05$ .

*Probability of transition between structural classes (Question 2).*—For gridded plots that burned, we determined probabilities of transition among structural classes (unburned plots did not change in identity). Pearson's chi-square tests ( $2 \times 2$  contingency tables) were used to compare the number of pre- and post-fire plots in each structural class, testing the null hypothesis that the proportions of plots among structural classes did not change after fire. *P*-values were based on a Monte Carlo simulation (Hope 1968, Patefield 1981), and significance was assessed at  $\alpha = 0.05$ .

*Effects of fire and burn severity on the size structure and composition of trees (Question 3).*—We used a combination of ordination, multivariate statistics, and comparisons of proportional mortality to explore how fire (and its severity) affected the size structure and composition of trees. Analyses were based on structural plots, which were stratified to capture variation in burning (burned vs. unburned areas) and initial vegetation structure (canopy cover) and sampled many more trees than did the smaller gridded plots.

We first used non-metric multidimensional scaling (NMDS; Kruskal 1964, Clarke 1993, McCune and Grace 2002) to illustrate graphically the variation in tree size structure (diameter distribution) of plots representing pre-fire structural classes (non-forest to closed forest) and how this changed with fire (or fire severity). For this analysis, structural-plot data were pooled from all sites. The sample matrix contained the densities of trees in each of five diameter classes in each plot, both before and after burning. Diameter classes varied in width:  $<5$  cm, 5 to  $<10$  cm, 10 to  $<20$  cm, 20 to  $<40$  cm, and  $\geq 40$  cm. Densities were square root-transformed, and the zero-adjusted Bray–Curtis distance was used as the dissimilarity measure (Bray

and Curtis 1957, Clarke et al. 2006), facilitating inclusion of samples without trees. Bray–Curtis has a constant maximum for samples with no elements in common and is a compromise between quantitative measures (e.g., Euclidean distance) that may not be robust to zero inflation and those based on presence–absence (e.g., Sorensen's distance; Clarke et al. 2006, Legendre and Legendre 2012). The ordination was based on 400 iterations with up to 40 random starting configurations that were tested until two similar solutions with minimum stress were found (McCune and Grace 2002, Oksanen et al. 2015). We chose the number of dimensions in the final solution based on a scree plot (i.e., a qualitative compromise between stress and dimensions; McCune and Grace 2002). The final solution was centered and rotated orthogonally to its principal components (sensu Legendre and Legendre 2012), resulting in highest dispersion of points along the first axis and progressively less dispersion along subsequent axes (Oksanen et al. 2015). Non-metric multidimensional scaling was run in the Vegan package using the metaMDS function (Oksanen et al. 2015) in the statistical program R (R Core Team 2016).

To aid interpretation of the ordination, we calculated Pearson's correlation coefficients between plot scores along each axis and the density of trees in each diameter class (as well as total density). To visualize the effects of fire on each of the pre-fire structural classes, we overlaid vectors on the ordination connecting the pre- and post-fire centroid of each structural class. Similarly, to visualize responses of structural classes to burn severity, we overlaid vectors connecting pre- and post-fire centroids of each structural  $\times$  burn-severity class.

We then tested the effects of fire on structure and composition through the multivariate responses of diameter classes and species, respectively. Differences in multivariate response were tested using the non-parametric method, PERMANOVA (Anderson 2001, Anderson and ter Braak 2003). We used site-specific PERMANOVA models to compare structure and composition before and after fire for burned plots. A second set of models, using post-fire data only, compared unburned plots to plots that burned at low, moderate, or high severity (single models followed by contrasts). The significance of individual contrasts was determined by an analogous permutational procedure. Prior to compositional analyses, we

removed *Tsuga mertensiana* (present in only two plots). We then relativized the data by species' maxima and plot totals to balance the weighting among species and samples (Bray and Curtis 1957, McCune and Grace 2002). For both the structural and compositional analyses, data were square root-transformed and the zero-adjusted Bray–Curtis distance was used as the dissimilarity measure (Bray and Curtis 1957, Clarke et al. 2006). PERMANOVAs were conducted using 999 permutations and implemented in the Vegan package (Oksanen et al. 2015) in the statistical program R (R Core Team 2016). To aid interpretation of these models, we computed for each size class and species the mean rate of mortality in plots representing each burn-severity class (low, moderate, and high) at each site.

## RESULTS

### Probabilities of burning and transitions among structural classes

*Distributions of burn severity (Question 1).*—Structural classes differed in the proportional representation of severity classes at Upper Bear and Helen Creek ( $P = 0.003$  and  $P < 0.001$ , respectively), but

did not differ at Hubbard and Butte Creeks ( $P = 0.83$  and  $0.14$ , respectively; Table 4). In general, non-forest was less likely to burn and forest was more likely to burn than expected, although the proportion of non-forest was small except at Helen Creek (Fig. 5). Open forest burned at high severity more frequently than did sparse woodland at all sites, except Helen Creek. Closed forest showed strikingly different burn-severity distributions in the two sites for which there were sufficient numbers of plots to make comparisons: Closed-forest plots most often burned at high severity at Hubbard Creek, but most often escaped fire at Butte Creek (Table 4).

*Transitions among structural classes (Question 2).*—At all sites, there was an increase in the proportion of non-forest plots and a decrease in the proportions of open- and closed-forest plots (Table 5; Fig. 5). The direction of change in sparse woodland varied among sites, increasing at Hubbard Creek and Upper Bear and decreasing at Helen and Butte Creeks (Fig. 5).

*Effects of fire on the size structure and composition of trees (Question 3).*—

1. *Changes in size structure.*—A three-dimensional NMDS solution proved optimal, jointly

Table 4. Proportions of gridded plots within each structural class (rows) that burned at each of four levels of severity (unburned to high severity).

Site and pre-fire structural class	$n^\dagger$	Unburned	Low	Moderate	High
Hubbard Creek: $\chi^2 = 3.15$ , $P = 0.83$					
Non-forest	1	—	—	—	—
Sparse woodland	16	0.25	0.12	0.25	0.38
Open forest	27	0.15	0.11	0.22	0.52
Closed forest	11	0.09	0.27	0.18	0.45
Butte Creek: $\chi^2 = 13.6$ , $P = 0.14$					
Non-forest	3	1.00	0.00	0.00	0.00
Sparse woodland	49	0.37	0.16	0.16	0.31
Open forest	28	0.18	0.32	0.21	0.29
Closed forest	3	0.67	0.00	0.33	0.00
Upper Bear: $\chi^2 = 19.9$ , $P = 0.003$					
Non-forest	5	0.60	0.20	0.20	0.00
Sparse woodland	36	0.06	0.17	0.31	0.47
Open forest	18	0.06	0.11	0.11	0.72
Closed forest	0	—	—	—	—
Helen Creek: $\chi^2 = 27.9$ , $P < 0.001$					
Non-forest	33	0.70	0.06	0.03	0.21
Sparse woodland	59	0.19	0.14	0.15	0.53
Open forest	21	0.19	0.19	0.14	0.48
Closed forest	0	—	—	—	—

Notes: Chi-square and  $P$ -values are from Pearson's chi-square tests;  $P < 0.05$  indicates that pre-fire structural classes differed in their proportional distributions of burn severity from the landscape as a whole. —, too few plots to analyze.

$^\dagger$  Number of plots in a structural class.

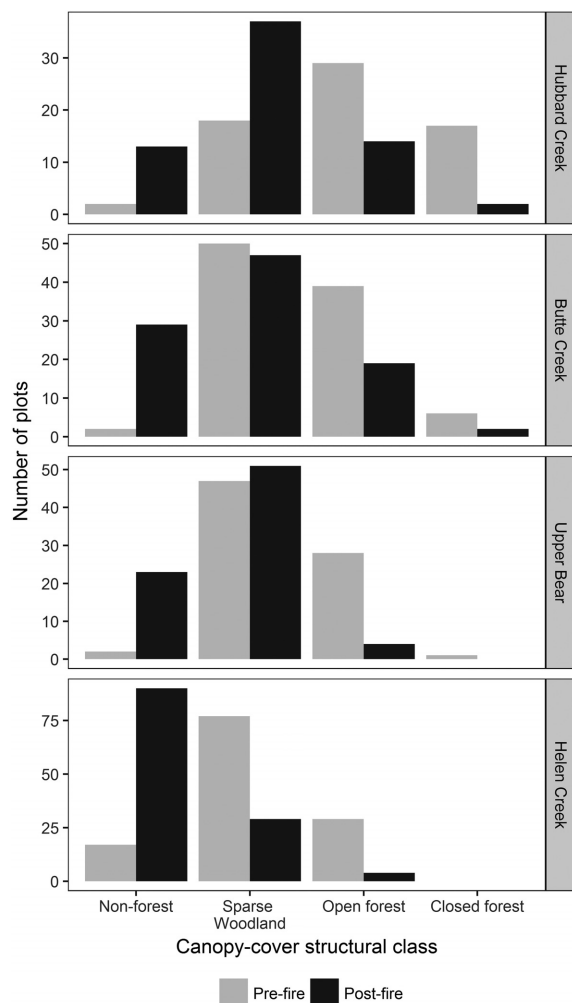


Fig. 5. Changes in the frequency of canopy-cover (structural) classes due to fire. Values are numbers of gridded plots; see Table 2 for total numbers of plots at each site.

minimizing stress (8.9) and number of dimensions. NMDS1 was negatively correlated with total tree density and density of smaller trees; NMDS2 was positively correlated with density of larger trees (Table 6). NMDS3 (not shown) was weakly correlated with most size classes (Table 6). Post-fire movement of structural classes in ordination space (top panel, Fig. 6) corresponded with reductions in total tree density (left to right along NMDS1) and in the relative densities of moderate and larger size trees (top to bottom along NMDS2), which showed proportionately greater mortality than did smaller trees (Fig. 7). Post-fire movement in ordination

space was minimal for unburned plots and increased with burn severity (bottom panel, Fig. 6), reflecting increasing mortality (reduced stem density) with severity, particularly in larger size classes (>20 cm dbh; Fig. 7).

PERMANOVA models confirmed statistically the interpretation of NMDS: Changes in diameter distributions due to fire were significant at three of the four sites (Table 7). Nearly all comparisons between unburned plots and those that burned at low, moderate, or high severity were highly significant (Table 7). There were three exceptions, however; structure did not differ between unburned and low-severity plots at Hubbard or Butte Creeks, or between unburned and moderate-severity plots at Hubbard Creek (Table 7).

2. *Changes in species composition.*—PERMANOVA models also indicated significant effects of fire on species composition (i.e., species' relative densities; Table 8). Eleven of sixteen models were significant, including the contrasts of pre- vs. post-fire plots and unburned vs. low-, moderate-, or high-severity plots. Similar to effects on structure, changes in composition were least evident at Hubbard Creek, where mortality rates were lowest (Fig. 8). Composition differed only between unburned and moderate- or high-severity plots. Although all species showed increasing mortality with burn severity (as expected), rates were as high or higher in *Pinus albicaulis* as in *Abies lasiocarpa* or *Picea engelmannii* (counter to expectation), even in plots that burned at moderate or low severity (Fig. 8). Mortality of *Larix lyallii* was low and largely limited to moderate-severity plots at Butte Creek. *Pinus contorta* and *Pseudotsuga menziesii*, montane species of limited distribution and abundance, suffered the highest rates of mortality (Fig. 8).

## DISCUSSION

A fundamental question about the effects of climate warming in the ATE is whether treeline will rise into previously treeless areas, or whether fire, other disturbances, and edaphic controls will maintain or increase the area of non-forest. With climate change, increases in fire size and severity could counter the expected upslope movement of trees into non-forested areas. If fire rarely burned into areas of non-forest or recent tree establishment, we would expect treeline to rise in direct



Table 5. Probabilities of transition (pre- to post-fire) among structural classes (gridded plots).

Fire	Pre-fire	<i>P</i>	Post-fire			
			Non-forest	Woodland	Open forest	Closed forest
Hubbard Creek	Non-forest	–	–	–	–	–
	Sparse woodland	0.41	0.25	0.75	0.00	0.00
	Open forest	0.76	0.17	0.65	0.17	0.00
	Closed forest	0.07	0.00	0.50	0.30	0.20
Butte Creek	Non-forest	–	–	–	–	–
	Sparse woodland	<0.001	0.32	0.68	0.00	0.00
	Open forest	<0.001	0.30	0.22	0.48	0.00
	Closed forest	0.002	0.00	1.00	0.00	0.00
Upper Bear	Non-forest	0.08	1.00	0.00	0.00	0.00
	Sparse woodland	1.00	0.29	0.71	0.00	0.00
	Open forest	0.13	0.24	0.76	0.00	0.00
	Closed forest	–	–	–	–	–
Helen Creek	Non-forest	0.007	1.00	0.00	0.00	0.00
	Sparse woodland	0.28	0.77	0.23	0.00	0.00
	Open forest	0.003	0.47	0.29	0.24	0.00
	Closed forest	–	–	–	–	–

Notes: *P* < 0.05 indicates a significant change in frequency of a structural class from pre- to post-fire based on a Fisher's exact test. –, too few plots to analyze.

response to climate warming (Fig. 1E, F). However, if fire burned at higher severity throughout the ATE, we would expect treeline to retreat (Fig. 1C, D). In our study, distributions of fire severity among structural classes suggest greater likelihood of the first scenario: Areas of non-forest or of smaller (presumably younger) trees were less likely to burn at higher severity than the landscape as whole. Nevertheless, distributions of fire severity and rates of tree mortality varied markedly within and among sites (Table 4, Fig. 8), in contrast to previous research in the ATE (Billings 1969, Agee and Smith 1984, Little et al. 1994, Stueve et al. 2009). For example, there was more high-severity fire and greater tree mortality in the two Northern Rockies sites than in the Cascade sites (Fig. 8). Similarly, associations between fire severity and canopy cover varied

among sites: Unburned areas and low-severity fire were associated with both non-forest and more dense forest in some sites (Butte Creek), but were strongly associated with non-forest only in the remaining sites (Table 4). Thus, our results suggest a third scenario: Changes in the ATE may be more complex and spatially variable than predicted by models of climate change and associated increases in the size or severity of disturbance (Fig. 9).

In our sites, high fuel moisture and reduced connectivity of surface and canopy fuels were likely responsible for the variability in fire severity and resulting variable mortality of trees. The higher fuel moisture of smaller trees likely contributed to their greater survival and dominance after fire. These structural changes are consistent with observations that younger subalpine stands burn less severely than older stands (Kulakowski and Veblen 2007), although the variation in size-related survival observed here occurred at smaller spatial scales (<10 m). Higher fuel moisture may also explain why closed forest at Butte Creek burned less than did more open forest or non-forest. Two characteristics of these denser-canopied forests probably contributed to higher surface-fuel moisture: their association with concave topography and greater shading of the forest floor. At a local scale, abiotic and biotic conditions that enhance surface-fuel moisture

Table 6. Pearson's correlation coefficients (*r*) between plot scores on NMDS axes and densities of trees in each diameter class.

Diameter class	NMDS1	NMDS2	NMDS3
<5 cm	–0.64	–0.38	–0.04
5 to <10 cm	–0.62	–0.12	–0.28
10 to <20 cm	–0.62	0.29	–0.25
20 to <40 cm	–0.50	0.50	0.27
≥40 cm	–0.24	0.29	0.26
All trees	–0.78	–0.11	–0.10

Note: NMDS, non-metric multidimensional scaling

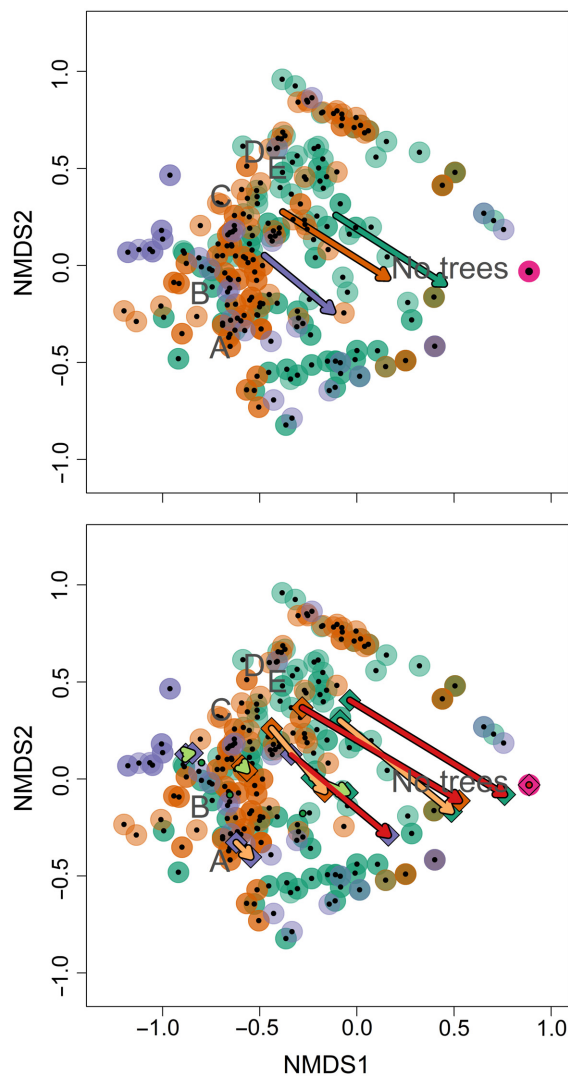


Fig. 6. Non-metric multidimensional scaling (NMDS) ordination of structural plots before and after fire based on density of trees in each of five diameter classes. The ordination was rotated to its principal components and centered. Upper panel emphasizes the change due to fire and the lower panel, the response to burn severity. Sample plots are coded by structural class: non-forest = pink, sparse woodland = teal, open forest = orange, and closed forest = violet. Arrows in the upper panel show change from pre- to post-fire for plots that burned; arrow colors correspond to structural classes. Arrows in the bottom panel connect pre- and post-fire centroids (diamonds) of structural classes that burned at differing severities. Centroid colors correspond to structural classes; arrow colors correspond to burn-severity classes: low severity (green), moderate severity

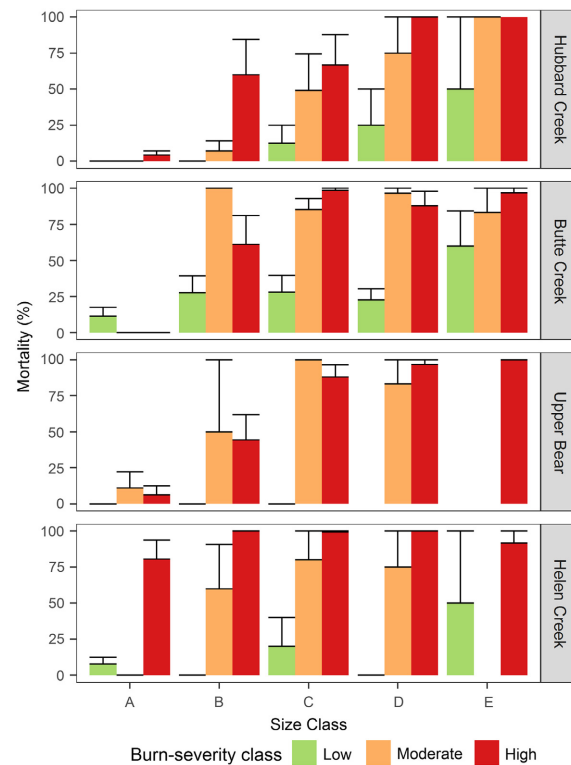


Fig. 7. Mortality (%) of trees of each size class (A-E) among burn-severity classes (low to high). Values are means + 1 SE. Black lines on the x-axis denote zero (0) mortality rather than the absence of trees (no lines). Size classes are defined in Fig. 6.

can exert strong bottom-up controls on fire severity in the ATE. As a result, effects of fire may be highly individualistic, dependent on initial forest structure and topographically driven variation in fuel moisture. Other research on fire effects on geomorphic processes in krummholz of the Northern Rockies illustrates similar within- and

(Fig. 6. *Continued*)

(orange), and high severity (red). Arrows indicate a consistent post-fire shift toward lower tree densities (right along NMDS1) and greater relative abundance of smaller trees (down along NMDS2) in all forested structural classes and burned plots regardless of severity. Unburned plots did not change from pre- to post-fire. In both panels, letters are the centroids of size (dbh) classes: A, <5 cm; B, 5 to <10 cm; C, 10 to <20 cm; D, 20 to <40 cm; and E, ≥40 cm.

Table 7. Results of PERMANOVA models testing for differences in the size (dbh) distributions of trees before and after fire (burned plots only) or among burn-severity classes (post-fire plots).

Predictor variable	Plots	Site	df	F	P
Pre- vs. post-fire	Burned	Hubbard Creek	1, 37	2.0	0.117
		Butte Creek	1, 79	9.6	0.001
		Upper Bear	1, 47	12.2	0.001
		Helen Creek	1, 81	43.3	0.001
Unburned vs. low severity	Post-fire	Hubbard Creek	1, 40	2.0	0.108
Unburned vs. moderate severity				1.9	0.129
Unburned vs. high severity				5.4	0.003
Unburned vs. low severity		Butte Creek	1, 59	1.3	0.275
Unburned vs. moderate severity				13.0	0.001
Unburned vs. high severity				9.0	0.001
Unburned vs. low severity		Upper Bear	1, 31	4.5	0.020
Unburned vs. moderate severity				5.3	0.011
Unburned vs. high severity				14.3	0.001
Unburned vs. low severity		Helen Creek	1, 56	13.3	0.001
Unburned vs. moderate severity				11.5	0.002
Unburned vs. high severity				31.7	0.001

Table 8. Results of PERMANOVA models testing for differences in the relative densities of tree species before and after fire (burned plots only) or among burn-severity classes (post-fire plots).

Predictor variable	Plots	Sites	df	F	P
Pre- vs. post-fire	Burned	Hubbard Creek	1, 379	0.5	0.684
		Butte Creek	1, 79	6.1	0.004
		Upper Bear	1, 47	8.3	0.002
		Helen Creek	1, 81	31.7	0.001
Unburned vs. low severity	Post-fire	Hubbard Creek	1, 40	2.0	0.144
Unburned vs. moderate severity			1, 40	2.4	0.072
Unburned vs. high severity			1, 40	2.5	0.06
Unburned vs. low severity		Butte Creek	1, 59	4.4	0.014
Unburned vs. moderate severity			1, 59	10.7	0.002
Unburned vs. high severity			1, 59	5.7	0.004
Unburned vs. low severity		Upper Bear	1, 31	1.8	0.165
Unburned vs. moderate severity			1, 31	3.5	0.034
Unburned vs. high severity			1, 31	9.8	0.001
Unburned vs. low severity		Helen Creek	1, 56	12.4	0.002
Unburned vs. moderate severity			1, 56	13.0	0.001
Unburned vs. high severity			1, 56	28.7	0.001

between-site variability (Stine and Butler 2015). A common characteristic of fire in the ATE is likely to be its mixed severity and variable effects on tree survival. Post-fire succession is thus likely to reflect the combined influences of initial structure, spatial variation in survival, and the reproductive patterns of survivors.

Climate and weather before and during fire should also influence patterns of burn severity. For example, burn severity was lower at Butte

Creek than at other sites (Table 4), which may have been due to higher than normal precipitation during the year of the fire (Table 1). Likewise, high precipitation may have contributed to the lack of burning in closed forest at Butte Creek, whereas low precipitation and a high climatic-moisture deficit may have contributed to the opposite pattern at Hubbard Creek (Table 1). That said, Helen Creek had higher than normal precipitation during the year of the fire, but had



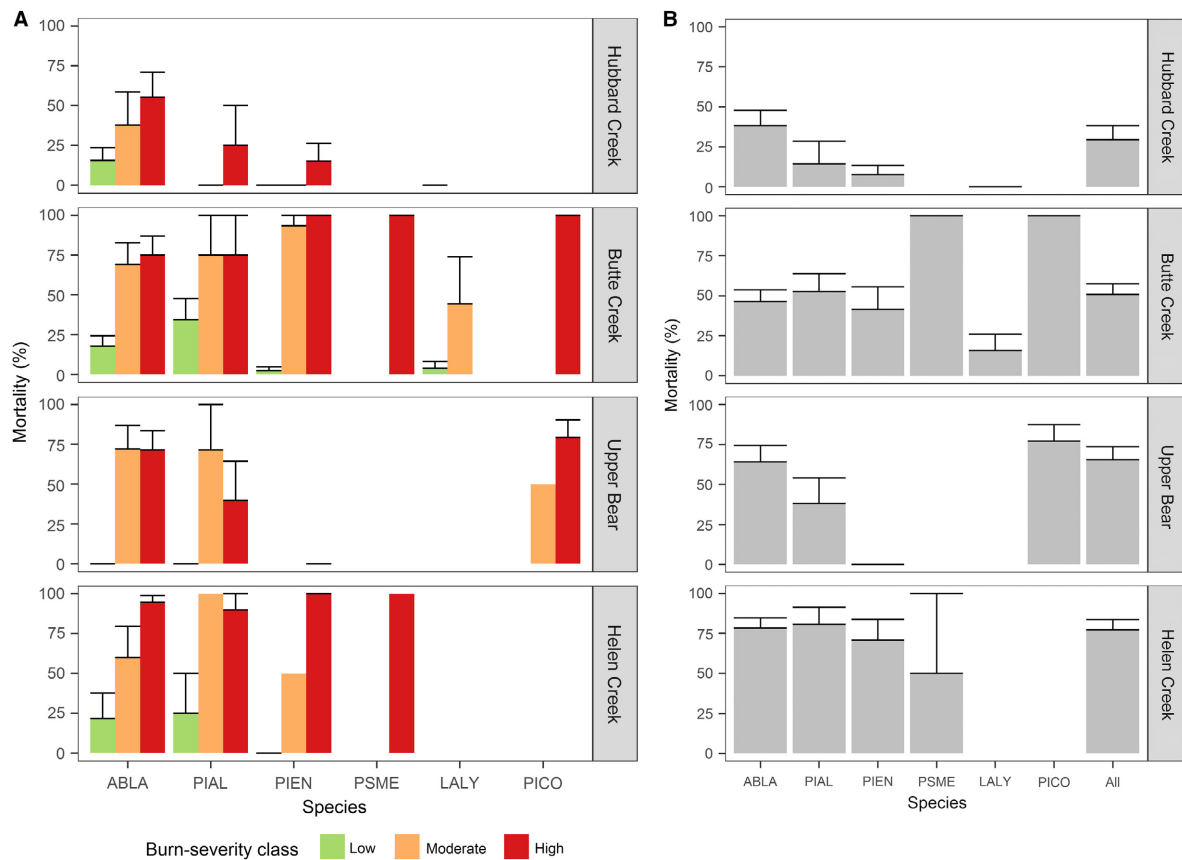


Fig. 8. Mortality (%) of the primary tree species among burn-severity classes (low to high; left column) and among all burned plots (right column). Values are plot means + 1 SE. Black lines on the x-axis denote zero (0) mortality rather than species' absence (no lines). Species codes are as follows: ABLA = *Abies lasiocarpa*, PIAL = *Pinus albicaulis*, PIEN = *Picea engelmannii*, PSME = *Pseudotsuga menziesii*, LALY = *Larix lyallii*, PICO = *Pinus contorta*, and All = all species.

a burn-severity distribution similar to Upper Bear and Hubbard Creek. The relationship between fire severity and annual climate can be complex—mediated by rates of snowmelt, soil moisture and water-holding capacity, length and severity of summer drought, and daily and hourly changes in weather during burning (Cansler and McKenzie 2014, Birch et al. 2015). Thus, a larger sample of burned ATEs and higher resolution climate and weather data would be necessary to understand how climate influences the severity and heterogeneity of fire in the ATE.

Species' relative susceptibility to fire differed, to some degree, from expectation. For example, *Larix lyallii* has been characterized as a "fire avoider," surviving in unburned refugia (Leiberg 1899, Agee 1993). At Butte Creek, where it was most

common, it survived in many plots that burned at low or moderate severity (counter to expectation). Field observations indicate that variation in fire severity, which aided its survival, occurred at spatial scales as small as 1–10 m. Conversely, *Pinus albicaulis* appeared more susceptible to fire than expected given its upright branching structure and thicker bark (Larson et al. 2009, Campbell et al. 2011). In fact, it often suffered comparable or greater mortality than *Abies lasiocarpa* or *Picea engelmannii* over the full range of burn severities. Similar responses to fire have been observed elsewhere in the Northern Rocky Mountains, where both *A. lasiocarpa* and *Pin. albicaulis* have experienced relatively high (>40%) mortality in prescribed fires (Keane and Parsons 2010). For *Pin. albicaulis*, high losses to fire may be indicative

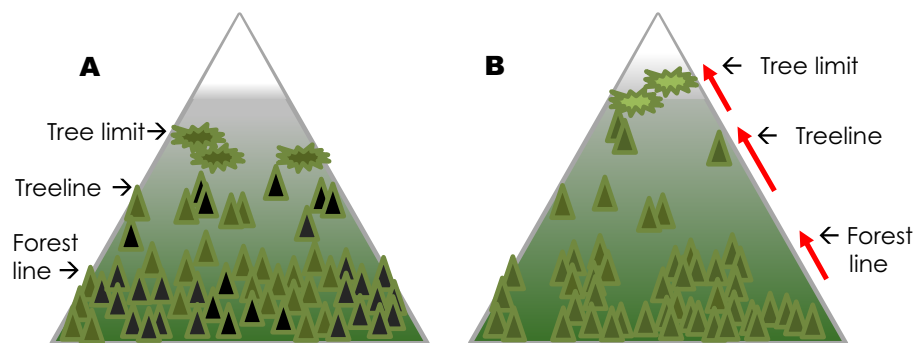


Fig. 9. Revised model of vegetation changes in the alpine treeline ecotone (ATE) with climate change, incorporating the effects of fire in this study (compare to conceptual model in Fig. 1). Fire that spreads through non-forest or ignites isolated tree islands (under more extreme fire behavior; A) would produce a wider, structurally more complex ATE (B). We observed this pattern in our Cascade Range and Northern Rocky Mountains sites. The models in Fig. 1 may still apply in other regions. For example, in regions where surface fuels limit fire spread (e.g., Sierra Nevada), Fig. 1E, F may be more representative. Likewise, in ATEs that abruptly transition to non-forest the ecotone may completely burn (Fig. 1C, D). As with mortality from fire, rates of tree establishment in response to climate change are likely to be spatially variable at both regional and local scales (Harsch et al. 2009, Harsch and Bader 2011).

of positive feedback among disturbance agents, that is, greater potential for ignition where trees suffer from other sources of stress or mortality (e.g., bark beetles or white pine blister rust). The possible feedbacks between previous mortality from biotic agents and subsequent mortality from fire warrant further investigation.

They may also have significant implications for the species: Trees that survive blister-rust infections can reinforce the rust resistance of pine populations, so their loss to fire will compromise the long-term conservation of the species (Keane et al. 2012). Current and future responses to fire may thus reflect the additive or synergistic effects of multiple disturbance agents and stressors, including invasive species and climate change (McKenzie et al. 2009, Smith et al. 2009).

Our results indicate that non-forested areas, including those below treeline, are less likely to burn than the open forests and sparse woodlands that dominate the ATE. A regional-scale analysis of burn patterns based on remote sensing and geospatial data found a similar result: Forested portions of the ATE burned 2.5 times as much as non-forest vegetation (Cansler et al. 2016). Sparse surface fuels or high fuel moisture likely limit the spread of surface fire in non-forested communities. Field observations indicated that many non-forested areas lacked charcoal, even when adjacent forests or smaller tree islands had burned severely.

Agee and Smith (1984) report similar patterns of patchy burning of subalpine parkland in the 1978 Hoh Fire in the Olympic Mountains (Washington state): “it burned through forested areas and tree clumps, skipping over subalpine meadows... [and over] meadow edges invaded by small trees.” Fire behavior that is extreme enough to produce fire brands may be important, and perhaps necessary, for fire to spread from closed forest to tree islands in the ATE. Although our geospatial analysis (Cansler et al. 2016) and field-based studies provide clear examples of fire in treed areas of the ATE, fire may not affect all treeline forms (e.g., krummholz or ribbon forests; but see Billings 1969, Stine and Butler 2015, Stine 2016) or environments, if surface fuels are limiting (e.g., Sierra Nevada or Great Basin; Arno and Hammerly 1984).

Our observations of susceptibility to burning in the ATE highlight an important aspect of fire in the Pacific Northwest and Northern Rocky Mountains: Non-forested areas serve as refugia from wildfires. Many alpine floras contain rare and endemic species (Körner 2003), which are better adapted to chronic abiotic stress than to infrequent disturbance by fire. The low flammability of non-forest areas may allow these species to persist even if climate change increases the frequency of fire in adjacent forests. Moreover, fire may actually expand or create new areas of non-forest from adjacent forest. Allowing fire to burn

in the ATE should be considered one of a number of climate-adaptation strategies available to natural resource managers. Additional research on the comparative effects of chronic stress (or other “press” disturbances) vs. wildfire (a “pulse” disturbance) on non-forest communities in the ATE would aid climate-change adaptation.

Even if climate warming facilitates tree encroachment into treeless portions of the ATE, concomitant increases in fire (and fire-induced mortality) could expand the area of non-forest (Fig. 9). In the short term (e.g., 20–100 yr), expansion of non-forest is likely if climate-mediated effects on fire outpace tree regeneration and growth. Still, the elevational limit of upright tree growth will likely rise as temperature-related constraints on growth are eased. Thus, krummholz and tree islands isolated in areas of non-forest at the climatic limits of upright tree growth may not burn, but should be responsive to warming. In sum, a climate-driven rise in treeline will not likely be counteracted by an increase in area burned. Instead, the ATE will likely widen, expanding bi-directionally, into closed forest due to fire and into alpine tundra as climatic controls on tree establishment are relaxed (Fig. 9).

As the ecotone widens, additional constraints may emerge that increase the complexity and spatial heterogeneity of vegetation types. For example, increasing distances to seed sources (at lower elevations in the ATE) may impose steep gradients in seed rain over the patchy spatial structure of vegetation left by mixed-severity fire (Haire and McGarigal 2010, Harvey et al. 2016, Stevens-Rumann et al. 2017). In mixed-conifer and sub-alpine forests, repeated wildfires or wildfires that occur soon after other disturbances can reduce the availability of seed, thus slowing post-fire regeneration (Harvey et al. 2013, Stevens-Rumann et al. 2015, Stevens-Rumann and Morgan 2016). In the ATE, increasing frequency of fire is likely to have similar effects. Increases in the extent or severity of fire may also create larger patches of disturbed forest that magnify or mask the finer-scale patterning generated by more typical fires (Cansler and McKenzie 2014). For most ecosystems, including the ATE, however, empirical data on the consequences of repeated fires are lacking (Prichard et al. 2017). Future studies should address how the spatial and temporal layering of fires and their interactions with other types of

disturbance and spatial processes (e.g., seed dispersal) are likely to shape the distribution and complexity of vegetation in the ATE.

## CONCLUSION

Previous research in the ATE has focused on the physiological mechanisms by which climate limits tree growth (Bansal and Germino 2008, Shi et al. 2008, Körner 2012), and how small-scale variation in topography or the presence of facilitators mediates environmental stress and tree establishment (Callaway et al. 2002, Maher and Germino 2006, Malanson et al. 2011). The potential consequences of climate change have broadened the scope of research in the ATE from physiological constraints of trees, to monitoring ongoing changes, projecting future responses to warming, and identifying ways to adapt to these changes. Although temperature constrains the elevational limits of trees, it is becoming clearer that other factors, including drought, edaphic controls, climatic history, chronic physical damage, and disturbance, impose additional limitations at both local and regional scales.

The state transitions documented in this study suggest that climate warming and increases in fire will generate spatially complex changes in the distribution and structure of vegetation in the ATE, rather than simple up or down movements of trees. In areas that burned, fire effects were moderate. Open forests and sparse woodlands were as likely to become non-forest as to maintain some tree cover; closed forests generally decreased in tree cover, but rarely changed to non-forest. Counter to expectation, larger trees were more susceptible to fire than were smaller trees. Overall, our results indicate that future changes in the structure and composition of ATEs in the Pacific Northwest and Northern Rocky Mountains will be highly variable, shaped, in large part, by the heterogeneity of fire effects. We expect the spatial complexity of vegetation to increase and the ecotone to widen, in response to the combination of fire effects with climatic influences on regeneration and growth (Fig. 9).

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