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Area burned in alpine treeline ecotones reflects region-wide trends

C. Alina Cansler[A,C], *Donald McKenzie*[B] *and Charles B. Halpern*[A]

[A]School of Environmental and Forest Sciences, University of Washington, Seattle, WA 98195-2100, USA.
[B]Pacific Wildland Fire Sciences Laboratory, USDA Forest Service, Seattle, WA 98103, USA.
[C]Corresponding author. Email: acansler@uw.edu

Abstract. The direct effects of climate change on alpine treeline ecotones – the transition zones between subalpine forest and non-forested alpine vegetation – have been studied extensively, but climate-induced changes in disturbance regimes have received less attention. To determine if recent increases in area burned extend to these higher-elevation landscapes, we analysed wildfires from 1984–2012 in eight mountainous ecoregions of the Pacific Northwest and Northern Rocky Mountains. We considered two components of the alpine treeline ecotone: subalpine parkland, which extends upward from subalpine forest and includes a fine-scale mosaic of forest and non-forested vegetation; and non-forested alpine vegetation. We expected these vegetation types to burn proportionally less than the entire ecoregion, reflecting higher fuel moisture and longer historical fire rotations. In four of eight ecoregions, the proportion of area burned in subalpine parkland (3%–8%) was greater than the proportion of area burned in the entire ecoregion (2%–7%). In contrast, in all but one ecoregion, a small proportion (≤4%) of the alpine vegetation burned. Area burned regionally was a significant predictor of area burned in subalpine parkland and alpine, suggesting that similar climatic drivers operate at higher and lower elevations or that fire spreads from neighbouring vegetation into the alpine treeline ecotone.

Additional keywords: alpine tundra, fire regime, infrequent disturbances, meadow, western North America.

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Introduction

Across western North America, the area burned and frequency of large wildfires declined in the middle of the 20th century, but both have increased since the 1970s. Annual variation in fire frequency and area burned in forest ecosystems throughout western North America is influenced, in part, by climate (Heyerdahl *et al.* 2008; Littell *et al.* 2009; Mori 2011; Abatzoglou and Kolden 2013). In the Pacific Northwest and Northern Rocky Mountains, the focal regions of the present study, significant increases in mean annual temperature, modest increases in precipitation, reductions in snowpack, earlier snowmelt, and a longer freeze-free season (Mote *et al.* 2005; Johnstone and Mantua 2014; Jolly *et al.* 2015) extend the fire season and increase area burned (Littell *et al.* 2009; Abatzoglou and Kolden 2013). These changes have occurred since 1900 (increasingly since 1980) and reflect both climate teleconnections (i.e. El Niño–Southern Oscillation and Pacific North American pattern) and anthropogenic influences (Abatzoglou *et al.* 2014; Johnstone and Mantua 2014). Further increases in area burned are expected due to anthropogenic climate change (Flannigan *et al.* 2009; Littell *et al.* 2010), which will interact with human-caused changes in the behaviour and severity of fires (Hessburg *et al.* 2015).

One biome in which the effects of climate change on fire regimes are poorly understood is the alpine treeline ecotone (ATE). This transitional zone extends from the upper edges of continuous subalpine forest to treeless alpine tundra. The ATE is characterised by two vegetation types: subalpine parkland, extending from the upper bounds of closed forest into the adjacent fine-scale mosaic of tree islands and non-forested vegetation (Rochefort *et al.* 1994); and alpine vegetation, non-forested areas supporting herbaceous meadow, shrub field, and alpine tundra.

We focus on the ATE for two reasons. First, it is expected to shift upward in direct response to climate change. Second, recent increases in area burned in subalpine forests have exceeded those in other forest types (Westerling *et al.* 2006; Cansler and McKenzie 2014; Reilly 2014; Harvey 2015; Zhao *et al.* 2015), suggesting that fire regimes in the subalpine may be more responsive to changes in climate than those at lower elevations. Climate warming is expected to force the ATE up in elevation. This has already occurred in some regions, but not in others (Harsch *et al.* 2009). Fire may counteract climate-driven changes, by removing forest cover and pushing the treeline down in elevation. When the ATE does burn, tree reestablishment may not occur if facilitators, such as whitebark pine (*Pinus albicaulis*), have been removed (Billings 1969), if local seed sources are limited (Agee and Smith 1984; Little *et al.* 1994), or if graminoids competitively exclude seedlings (Stahelin 1943). Conversely, fire may hasten the upward movement of treeline by reducing competition from herbaceous species, as observed in arctic treelines (Brown 2010). Thus, although fire may occur infrequently, its effects can be profound and persistent.

How the direct effects of climate in the ATE may be modified by climate-driven changes in fire regime remains an unanswered question. Fires occur infrequently near the treeline and are extremely rare in Krummholz and alpine tundra (Arno and Hammerly 1984; Benedict 2002; Körner 2003). There are few studies of fire frequency in these systems (Douglas and Ballard 1971; Potash and Agee 1998), likely because fires are infrequent or absent (Malanson *et al.* 2007; Baker 2009). In contrast, in non-forested areas in or adjacent to subalpine parkland, fire frequencies may be similar to neighbouring subalpine forests (Gabriel 1976; Agee 1993; Baker 2009). In a warming climate, area burned may increase in subalpine forests more than in other forest types because climate is the principal driver of variability in high-severity fire regimes (those characteristic of montane, subalpine and boreal forests; Turner and Romme 1994; Bessie and Johnson 1995). Fuel condition (flammability) is a limiting factor, but fuel abundance and connectivity are not (Littell *et al.* 2009; Mallek *et al.* 2013).

Two opposing forces can affect area burned in the ATE. Increasing burned area may be driven by more contagious fuels and more frequent fire in adjacent subalpine forests. In contrast, the spread of fire from adjacent forests into the ATE may be inhibited by meadows with higher fuel moisture or by sparsely vegetated or barren areas. Thus, it is possible that ATEs may be responsive to climate-driven increases in regional area burned, or alternatively, may be buffered from them. To determine whether recent regional climate-driven increases in area burned have affected the ATE, we calculated the total area and temporal trends in wildfire in subalpine parkland and alpine vegetation for eight ecoregions of the Pacific Northwest (Cascade Range) and Northern Rocky Mountains for a 29-year period spanning 1984 to 2012. Separate analyses among ecoregions provide a comparison of burning among geographic locations with differing climates and fire years (Littell *et al.* 2009; Abatzoglou and Kolden 2013). We addressed the following questions:

1. How much area in subalpine parkland and alpine vegetation burned during the study period?
2. Can annual area burned in subalpine parkland and alpine vegetation be predicted from area burned in the region as a whole?
3. Do subalpine parkland and alpine vegetation burn proportionally more, less, or the same as the region as a whole?
4. Was there a temporal trend in the proportion of area burned in subalpine parkland and alpine vegetation during the past three decades?

Methods

Study area

The study area includes mountainous ecoregions in the Pacific Northwest and Northern Rocky Mountains among the states of Oregon, Washington, Idaho, Montana and Wyoming (Fig. 1). We identified these as areas within the Level I Commission for Environmental Cooperation Ecoregion 'North-western Forested Mountains,' and the Level II Ecoregion 'Western Cordillera' (Commission for Environmental Cooperation 1997). Within the latter, the analysis was constrained to state boundaries and eight Level III Ecoregions having the majority of their areas within these five states (Fig. 1).

From west to east, the study area comprises a gradient from maritime mesic to dry continental climates. Major high-elevation tree species west of the Cascade Range (Cascades and North Cascades) include *Abies lasiocarpa* (subalpine fir) and *Tsuga mertensiana* (mountain hemlock) (Arno and Hammerly 1984; Franklin and Dyrness 1988; nomenclature follows United States Department of Agriculture, Natural Resources Conservation Service 2015). East of the Cascade Crest and in the Rocky Mountains, high-elevation subalpine species include *A. lasiocarpa* and *Picea engelmannii* (Engelmann spruce), with *Larix lyallii* (subalpine larch) and *Pinus albicaulis* (whitebark pine) more prevalent near treeline (Arno and Hammerly 1984). East of the Continental Divide in the Middle Rockies, *Pinus contorta* var. *latifolia* (lodgepole pine) is found at high elevations near the treeline (Arno and Hammerly 1984).

Historical fire rotations – the time needed to burn an area equal to that of the analysis area – in dry subalpine forests and parklands ranged from 100 to 275 years in the Cascade Range (Fahnestock 1976; Franklin *et al.* 1988; Agee *et al.* 1990) and from 175 to 350 years in the Northern Rocky Mountains (Baker 2009). In the latter, rotations were slightly shorter in Montana and Idaho (~150–250 years) than east of the Continental Divide in Wyoming and Colorado (~250–350 years) (Baker 2009). Some forest types, such as *P. albicaulis*–*A. lasiocarpa* had shorter fire intervals (50–100 years) in some regions (e.g. the Idaho Batholith; Arno and Petersen 1983), whereas other subalpine forest types, such as mountain hemlock, had much longer historical fire rotations (>1500 years; Arno and Habeck 1972; Franklin and Dyrness 1988; Lertzman and Krebs 1991; Agee 1993).

ATEs in all ecoregions have non-forested vegetation, including alpine tundra, alpine fellfields, shrub fields (particularly *Vaccinium* and heather species), and meadows. The most common vegetation types vary among regions: forb-dominated wet meadows and shrub fields in the Cascade Range, graminoid-dominated communities east of the Cascade Range and in the Rocky Mountains, and low-statured alpine tundra east of the Continental Divide. Despite this variation, there are many similarities among ecoregions, particularly those from the eastern slopes of the Cascade Range to the western side of the Continental Divide (Ayres 1900; Daubenmire 1952, 1968; Gabriel 1976; Franklin and Dyrness 1988).

Geospatial data

We identified subalpine parkland and alpine vegetation from the US Geological Survey 'Gap Analysis Landcover' layer (National Gap Analysis Program 2011); together these two vegetation types make up the alpine treeline ecotone. The Gap Analysis Landcover layer models natural vegetation at 30-m resolution in hierarchical classes. It is derived from multisensor satellite imagery, digital elevation models, and topographical data (Kagan *et al.* 2005). We created subalpine parkland and alpine vegetation layers from the finest scale of vegetation described (Table 1). For the present study, the alpine layer included non-forested vegetation (e.g. alpine shrub fields) immediately adjacent to subalpine parkland and high alpine tundra distant from the

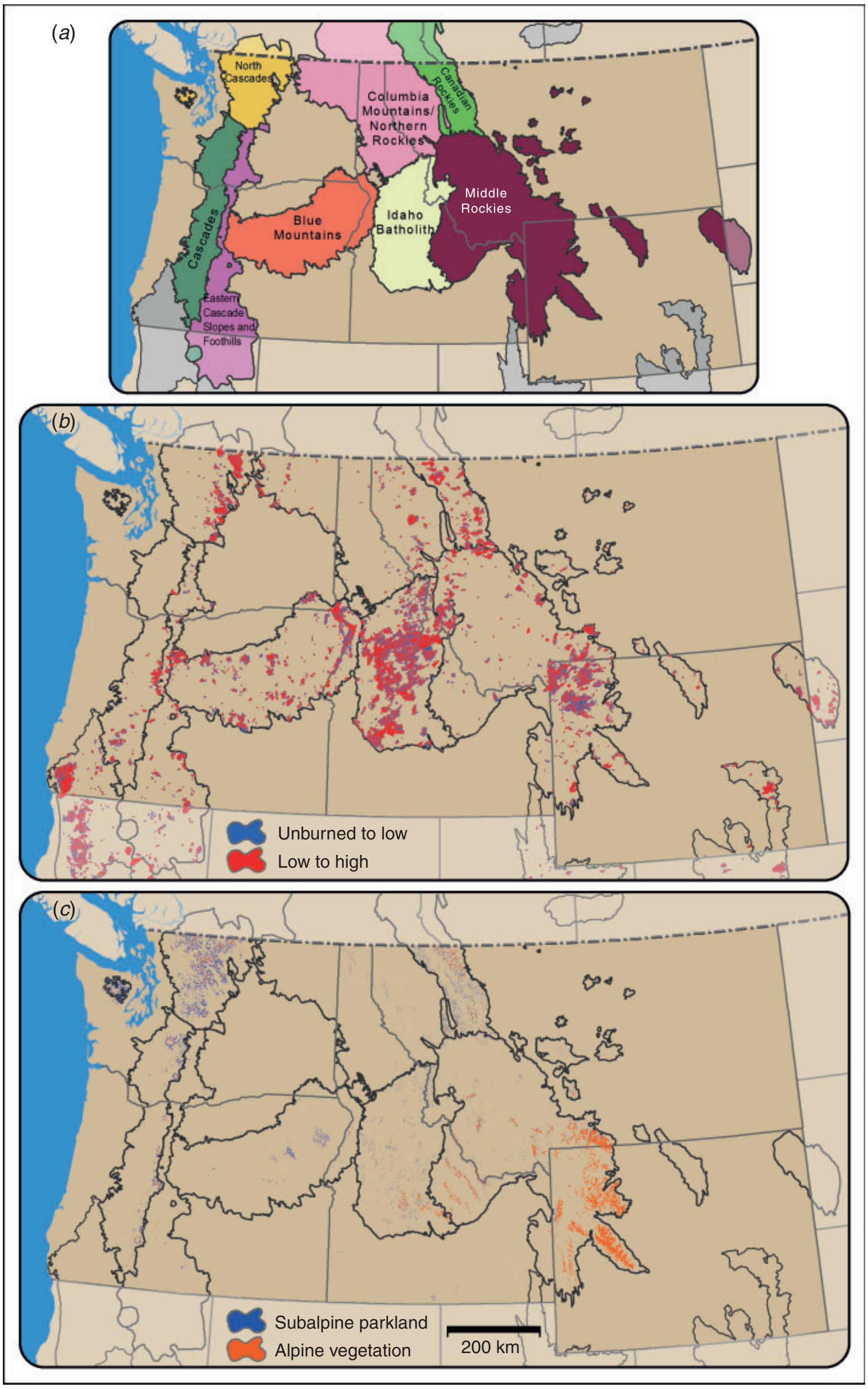

Fig. 1. Map of study area. (*a*) Level III Commission for Environmental Cooperation (1997) Ecoregions included in the analysis. Level III Ecoregions were within 'Western Cordillera' Level II Terrestrial Ecoregion (shaded grey), and had the majority of their area within the five Pacific Northwest and Northern Rocky Mountains states: Oregon, Washington, Idaho, Montana and Wyoming. (*b*) Classified burn-severity images for all fires >400 ha from 1984 to 2012 within the 'Western Cordillera' Commission for Environmental Cooperation (1997) Level II Terrestrial Ecoregion. (*c*) Subalpine parkland and alpine vegetation classes; together, these classes make up the alpine treeline ecotone. Burned area within the five-state analysis area within the Western Cordillera was assessed in this study.

Table 1. Vegetation classes from the Gap Analysis Landcover data used to identify subalpine parkland and alpine vegetation
Data have a 30-m resolution. Area values are the totals for the eight Level III ecoregions

Vegetation class	Area (ha)	Level I class	Level II class	Level III class
Subalpine parkland	493 138	Forest and woodland	Conifer-dominated forest and woodland (xeric–mesic)	Northern Rocky Mountain subalpine woodland and parkland
Subalpine parkland	92 930	Forest and woodland	Conifer-dominated forest and woodland (xeric–mesic)	Rocky Mountain subalpine–montane limber–bristlecone pine woodland
Subalpine parkland	209 141	Forest and woodland	Conifer-dominated forest and woodland (mesic–wet)	North Pacific maritime mesic subalpine parkland
Alpine	21 645	Shrubland, steppe and savanna	Alpine and avalanche–chute shrubland	North Pacific dry and mesic alpine dwarf-shrubland, fell-field and meadow
Alpine	114 146	Shrubland, steppe and savanna	Alpine and avalanche–chute shrubland	Rocky Mountain alpine dwarf-shrubland
Alpine	24 071	Shrubland, steppe and savanna	Alpine and avalanche–chute shrubland	Rocky Mountain alpine tundra, fell-field, and dwarf-shrubland
Alpine	210 269	Grassland	Alpine grassland	Rocky Mountain alpine fell-field
Alpine	609 469	Grassland	Alpine grassland	Rocky Mountain dry tundra
Alpine	49 309	Grassland	Alpine grassland	North Pacific alpine and subalpine dry grassland

Table 2. Area of subalpine parkland and alpine vegetation within each ecoregion
Ecoregions are shown in Fig. 1*a*

Ecoregion	Total (ha)	Subalpine (ha)	Alpine (ha)	Proportion in subalpine parkland	Proportion in alpine vegetation
Blue Mountains	7 091 151	42 918	5099	0.006	0.001
Canadian Rockies	5 693 431	109 612	41 864	0.019	0.007
Cascades	4 643 400	84 913	21 346	0.018	0.005
Columbia Mountains–Northern Rockies[A]	13 744 447	22 116	102	0.002	0.000
Eastern Cascades Slopes and Foothills[B]	5 617 714	8294	1834	0.001	0.000
Idaho Batholith	6 028 341	77 293	43 274	0.013	0.007
Middle Rockies	16 446 161	89 754	842 103	0.005	0.051
North Cascades	3 681 462	349 293	72 058	0.095	0.020
Study area	62 946 106	784 193	1 027 680	0.012	0.016

[A]Hereafter 'Columbia Mountains', to avoid confusion with the larger Northern Rocky Mountain region. The latter encompasses four ecoregions: Canadian Rockies, Columbia Mountains, Idaho Batholith and Middle Rockies.
[B]Hereafter 'Eastern Cascades'.

nearest closed subalpine forest. Two ecoregions, Eastern Cascades and Columbia Mountains, had little parkland and very little (<1% of the area) high-elevation, non-forested vegetation (Table 2); thus, we did not include alpine vegetation in analyses of those regions.

The vegetation layers used in this study are conservative representations of two vegetation landcover classes in the ATE. To exclude closed forests, we had to exclude mountain hemlock forests and montane grasslands that may have occurred in the lower bands of some ATEs. We also excluded barren areas (ice, water and rock) common at high elevations that do not burn; including them would have underestimated the proportion of area burned. To confirm accurate representation of the two primary vegetation classes in the ATE, we used high-resolution (1- to 2-m) imagery in Google Earth Pro (Google Inc. 2013) to ensure that no large areas of alpine tundra, meadow, or subalpine parkland were missed and that no source vegetation classes included large areas of closed forest.

We obtained geospatial fire data from the 'Monitoring Trends in Burn Severity' (MTBS) Program (Eidenshink *et al.* 2007; Monitoring Trends in Burn Severity 2014). Data were used to calculate area burned across all vegetation types and within subalpine parkland and alpine vegetation for each year of the study period (1984–2012). MTBS data include all fires >400 ha. They are generated from fire perimeters from federal and state fire databases and a Landsat-derived index of burn severity, the differenced Normalized Burn Severity Ratio (dNBR). DNBR is computed as change from pre- to post-fire in the surface spectral reflectance of the near- and mid-infrared bands of Landsat satellite imagery (Key 2006). It is correlated with field-based measures of burn severity and tree mortality in the Pacific Northwest and Rocky Mountains (Cansler and McKenzie 2012; Parks *et al.* 2014).

We did not use the MTBS data to quantify severity *per se*, but took advantage of the severity classification to compare the sensitivity of our estimates to the inclusion of areas classified as 'unburned to low'. We first computed the area burned based on the area classified in the MTBS burn-severity data as anything other than 'unburned to low' (i.e. the sum of low, moderate, high, increased greenness and unclassified; Eidenshink *et al.* 2007). Excluding classes 'unburned to low' should yield a more accurate estimate because it excludes large unburned areas that are often included in estimates derived from remotely sensed fire perimeters (Kolden *et al.* 2012, 2015). These errors of inclusion may be even higher for the ATE because fire perimeters are often extended to the nearest major topographical break (e.g. a ridgetop) (Kolden and Weisberg 2007; Cansler 2011) and may include unburned wet and barren alpine areas. For comparison, we computed the entire area within a fire perimeter (i.e. all severity classes; see online supplementary material). By reporting both estimates, we bound the uncertainty due to misclassification and inaccurate perimeters, although it is likely that some inaccuracies remain.

Statistical analyses

For each analysis, we computed values for the eight ecoregions combined (hereafter 'study area') and for each ecoregion individually to assess regional variation. Analyses were limited to ecoregions in which subalpine or alpine vegetation made up at least 0.1% of the landscape.

Question 1: Area burned in subalpine parkland and alpine vegetation

For subalpine parkland and alpine vegetation, we calculated the total area, total area burned, and proportion of area burned annually and over the entire study period.

Question 2: Relationship to area burned in the region as a whole

We used simple linear regression to test if the total area burned annually was a significant ($\alpha = 0.05$) predictor of area burned in subalpine parkland or alpine vegetation, allowing comparisons of slopes and variance explained among ecoregions. Area data were log-transformed ($\log(1+x)$) to stabilise the variance. We assessed whether data met the assumptions of regression using standard methods (e.g. normal probability plots, residual plots, and partial residual plots; Kutner *et al.* 2005). For this analysis, we chose to include subalpine parkland and alpine vegetation in estimates of area for the region as a whole; for most ecoregions, they accounted for <2% of the total area (Table 2), thus had minimal effect on regional totals.

Question 3: Area burned relative to area burned in the region as a whole

We tested the null hypothesis that burning in the subalpine and alpine occurred in proportion to that of the region as a whole. Failure to reject the hypothesis would imply that any distinctive fuel or climatic conditions in the ATE do not influence the potential to burn. If burning was less in the ATE than in the region as a whole, it would suggest that despite regional increases in area burned since the mid-1980s, limited fuel connectivity, shorter fire seasons or elevational differences in microclimate still limit burning (Littell *et al.* 2009). Finally, if burning was greater in the ATE than in the region as a whole, it would suggest that fuels are more flammable or the ATE is more exposed to fire from neighbouring vegetation types. To assess these alternative outcomes, we compared proportions of area burned in subalpine parkland and alpine vegetation with proportions of area burned across all vegetation classes ('expected area burned' in statistical comparisons; Cumming 2001; Podur and Martell 2009). We first compared these proportions for the entire study period. Then, using individual years as samples ($n = 29$), we tested whether proportions differed statistically using the Wilcoxon signed rank test with the two-tailed null hypothesis that the observed area burned did not differ from the expected ($\alpha = 0.05$).

Question 4: Temporal trends in area burned

To determine if there was a temporal trend in the proportion of area burned in subalpine parkland or alpine vegetation during the study period, we tested the linear relationship between log-transformed area burned and year ($\alpha = 0.05$). Separate models were developed for the study area as a whole and for each ecoregion. We interpreted any trends with caution because the sample size is small ($n = 29$) and a deviation in a single year may influence results. All tests were conducted in the statistical program *R* (R Core Team 2014).

Results

Question 1: Area burned in subalpine parkland and alpine vegetation

Subalpine parkland made up 1.2% of the study area (784 193 ha; Table 2) and 7% (55 137 ha) burned during the study period (Table 3). Alpine vegetation made up 1.6% of the area (1 027 680 ha) and 3% (27 501 ha) burned during the study period. In alpine vegetation, the proportion of area burned was very low (Table 3), consistent with long fire rotations from historical studies. Ecoregions with greater proportions of subalpine parkland and alpine vegetation (Table 2) usually had higher proportions burned (Table 3). The Middle Rockies was an exception: only 3% of the alpine burned despite covering >5% of the area. Regions with larger proportions of area burned also had larger proportions of alpine or subalpine parkland burned. For example, in the Blue Mountains, a higher proportion of the total area burned (11%), as did the alpine (19%), even though the alpine covered only 0.1% of the landscape (Table 2). Likewise, in the Idaho Batholith, 29% of the total area burned, as did a large proportion (22%) of subalpine parkland.

Question 2: Relationship to area burned in the region as a whole

Linear regressions predicting subalpine or alpine area burned from total area burned were significant for all but one ecoregion ($P < 0.01$; Table 4). For the entire study area, models explained 84% (subalpine) and 76% (alpine) of the variance ($P < 0.001$). For individual ecoregions, significant models explained 28%–88% of the variance. Greater variation was explained, and slopes were generally steeper, in ecoregions where more area burned (e.g. Canadian Rockies and Idaho Batholith).

Table 3. Area (ha) and proportion of area burned over the 29-year study period for subalpine parkland, alpine vegetation and the region (total)

Ecoregion	Area burned (ha)			Proportion burned		
	Subalpine parkland	Alpine vegetation	Total area	Subalpine parkland	Alpine vegetation	Total area
Blue Mountains	3722	942	769 493	0.087	0.185	0.109
Canadian Rockies	8863	531	317 990	0.081	0.013	0.056
Cascades	3268	381	140 947	0.038	0.018	0.030
Columbia Mountains	695	0	240 568	0.031	0.004	0.018
Eastern Cascades	211	24	303 403	0.025	0.013	0.054
Idaho Batholith	17 013	1525	1 757 879	0.220	0.035	0.292
Middle Rockies	7162	23 469	1 191 033	0.080	0.028	0.072
North Cascades	14 201	638	294 374	0.041	0.009	0.080
Study area	55 137	27 510	5 015 686	0.070	0.027	0.080

Table 4. Results of linear regressions predicting annual area of subalpine parkland or alpine vegetation burned as a function of annual total area (all vegetation types) burned ($n = 29$)

Bold font indicates a significant relationship. Data were log-transformed before analysis

Ecoregion	Subalpine parkland					Alpine vegetation				
	Intercept	Slope	t	P	R^2	Intercept	Slope	t	P	R^2
Blue Mountains	−3.76	0.65	4.76	**<0.001**	0.32	−2.41	0.44	3.24	**0.001**	0.28
Canadian Rockies	−0.23	0.58	8.33	**<0.001**	0.85	−0.23	0.28	4.12	**<0.001**	0.55
Cascades	0.00	0.42	5.85	**<0.001**	0.55	−0.11	0.30	4.22	**<0.001**	0.67
Columbia Mountains[A]	−0.65	0.26	2.93	**0.004**	0.28	–	–	–	–	–
Eastern Cascades[A]	−0.54	0.17	1.67	0.096	0.14	–	–	–	–	–
Idaho Batholith	−3.51	0.83	6.74	**<0.001**	0.68	−2.85	0.48	3.94	**0.002**	0.35
Middle Rockies	−2.77	0.63	5.66	**<0.001**	0.47	−3.15	0.72	6.58	**<0.001**	0.45
North Cascades	−0.46	0.61	7.78	**<0.001**	0.62	−0.53	0.24	3.06	**<0.001**	0.33
Study Area	−10.17	1.44	7.31	**<0.001**	0.84	−10.57	1.34	6.90	**<0.001**	0.73

[A]Alpine vegetation in the Columbia Mountains and Eastern Cascades ecoregions was not analysed because it occupied too small an area.

Question 3: Area burned relative to area burned in the region as a whole

For the entire study area and study period, the proportion of subalpine parkland burned was less than proportion of total area burned (7% vs 8%, respectively; $P = 0.031$; Table 3). However, in some years, a greater proportion of subalpine parkland burned, particularly when the total area burned was high (Figs 2 and 3; Table 5).

We observed considerable variation in burning among ecoregions. Over the 29-year study period, a larger proportion of subalpine parkland burned than the region in four of the eight ecoregions (Canadian Rockies, Cascades, Columbia Mountains and Middle Rockies; Table 3). Annually, the proportion of subalpine parkland that burned did not differ from regional area burned in two ecoregions (Canadian Rockies and Cascades), but was lower in the remaining six (Table 5).

Across the entire study area and in all ecoregions except the Blue Mountains, the proportion of alpine vegetation that burned was smaller than the regional area burned for the entire study period (Table 3) and annually (Table 5). There was one exception: in the Blue Mountains, a greater proportion of alpine vegetation burned than in the region as a whole (19% vs 11%), but the difference was not significant when tested with annual data ($P = 0.142$).

Question 4: Temporal trends in area burned

We did not detect a temporal trend in the proportion of area burned over the study period, with the exception of the Idaho Batholith (significant increase, $P < 0.001$).

Comparison with results derived from fire perimeters

Analyses based on area burned within fire perimeters (rather than area of higher burn-severity classes) did lead to large differences in estimates of total area burned (Table S1, available as online supplementary material), but rarely changed statistical outcomes (Tables S2 and S3). The only exception was for the proportion of subalpine parkland burned for the entire study area. It did not differ from the total area burned based on fire perimeters (Table S2), but it was significantly smaller based on higher burn-severity classes (Table 5). Even when area estimates differed greatly, model outcomes did not change. In the most extreme case, use of fire perimeters more than doubled the alpine area burned (Middle Rockies, 23 469 vs 58 644 ha).

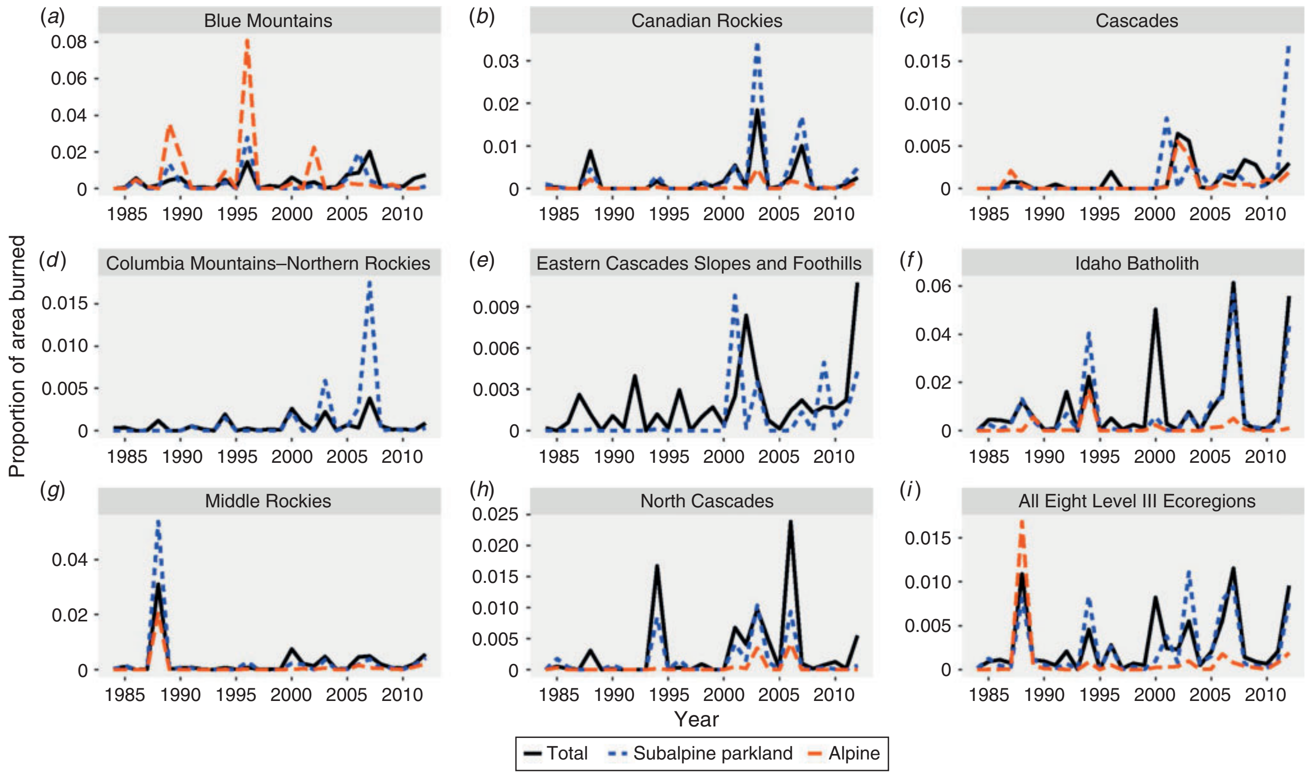

Fig. 2. Time series of area burned (regional, subalpine parkland and alpine vegetation) for each ecoregion (*a–h*), and across the entire study area (*i*).

Table 5. Results of Wilcoxon signed rank tests comparing annual proportions burned in subalpine parkland or alpine vegetation with expected proportions (i.e. annual proportion burned of all vegetation types)

V is the test statistic. Non-significant results support the null hypothesis that area burned in subalpine parkland or alpine vegetation was in proportion to that of the region as a whole. Significant results (bold font) with a negative median support the hypothesis that subalpine parkland or alpine vegetation was less likely to burn than the region. There were no significant tests with a positive median (greater likelihood of burning in the subalpine or alpine)

Ecoregion	Subalpine parkland			Alpine vegetation		
	V	*P*	Estimated median	*V*	*P*	Estimated median
Blue Mountains	86	**0.008**	−0.0010	138	0.142	−0.0006
Canadian Rockies	102	0.237	0.0004	2	**<0.001**	−0.0010
Cascades	58	0.623	−0.0003	18	**0.010**	−0.0007
Columbia Mountains[A]	76	**0.036**	−0.0002	.	.	.
Eastern Cascades[A]	47	**0.001**	−0.0010	.	.	.
Idaho Batholith	84	**0.007**	−0.0011	0	**<0.001**	−0.0041
Middle Rockies	73	**0.006**	−0.0003	0	**<0.001**	−0.0009
North Cascades	50	**0.024**	−0.0011	0	**<0.001**	−0.0024
Study area	117	**0.031**	−0.0003	26	**<0.001**	−0.0013

[A]Alpine vegetation in the Columbia Mountains and Eastern Cascades ecoregions was not analysed because it occupied too small an area.

Discussion

This study provides the first regional-scale assessment of area burned that focuses on the ATE. Other studies using geospatial approaches have assessed area burned at broader scales, e.g. the western US, and have established relationships to climate (Littell *et al.* 2009; Littell and Gwozdz 2011; Abatzoglou and Kolden 2013) and to fire management and forest type (Miller *et al.* 2012; Mallek *et al.* 2013). Most previous research on fire regimes in high-elevation forests and the ATE has used dendrochronological methods. Although these provide a long temporal record of the mean and variation in fire frequency, inferences about area burned are difficult, even with many field sites. This study bridges the gap between large-scale analysis of fire – spanning multiple vegetation types in the subalpine and

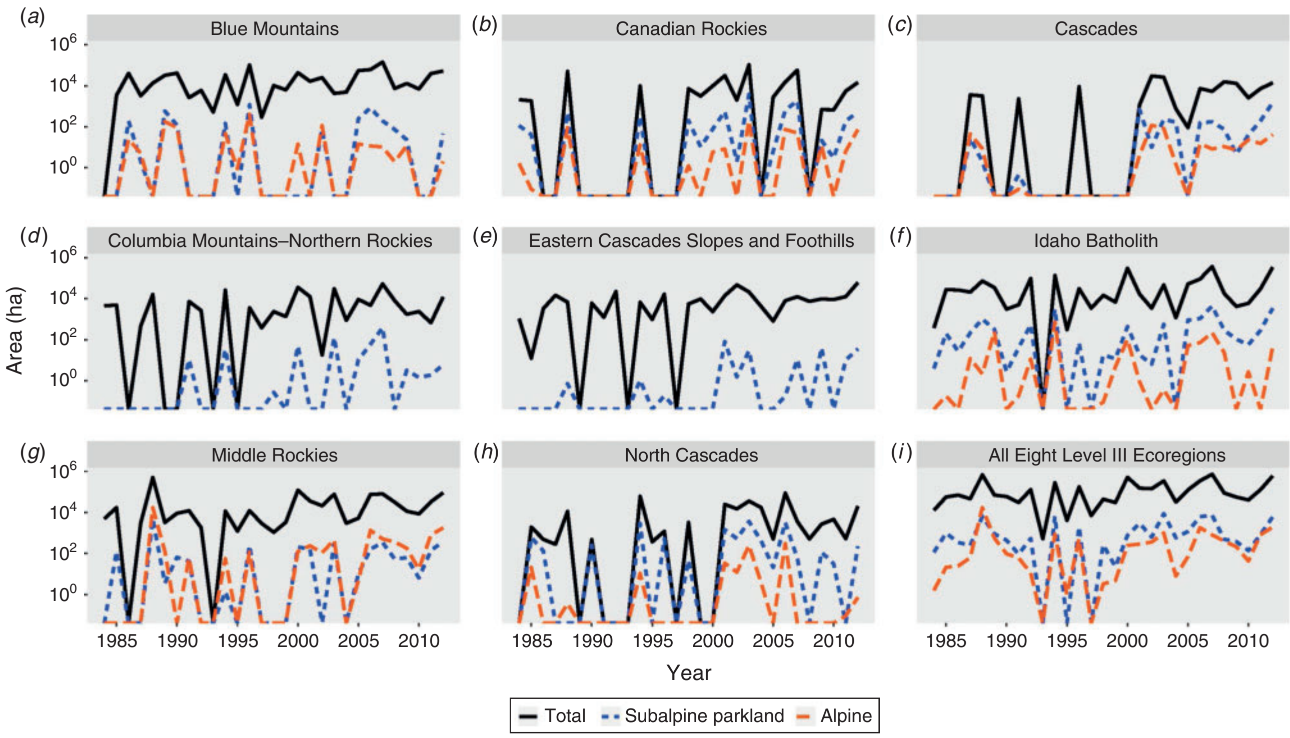

Fig. 3. Time series of the proportion of area burned (regional, subalpine parkland and alpine vegetation) for each ecoregion (*a–h*), and across the entire study area (*i*). Note that the scales of the *y* axes vary.

alpine – and previous smaller-scale work. It characterises type-specific patterns, but at large spatial extents, i.e. ecoregions in the Pacific Northwest and Northern Rocky Mountains.

Comparisons of proportion of area burned

An important and surprising result of this study was that proportionally, the area of subalpine parkland burned was greater than the total area burned in four of the eight ecoregions (Canadian Rockies, Cascades, Columbia Mountains, and Middle Rockies). This result runs counter to our understanding of historical fire rotations in these ecosystems: before Euro-American settlement, subalpine parkland generally had longer fire rotations than did other forest types (175–350 years in the Northern Rockies and Interior Northwest; see summaries in Agee 1993; Baker 2009). There are several possible explanations for this result: (1) effects of a changing climate; (2) spread from other fire-prone forest types at lower elevations; (3) increasing 'wildland fire use' on public lands (i.e. allowing fires to burn for resource benefit); and (4) reduced area burned at low elevations compared with the presettlement period. We discuss each of these mechanisms below, and suggest how future research could provide insight into their relative importance. Explicit comparison of these alternative mechanisms awaits more complete databases than are currently available, and a coarser-grained study that would cover a much larger geographic domain.

Effects of changing climate

Changes in climate in the study area, including increased mean annual temperature, decreased summer and autumn precipitation, reduced snowpack, and earlier snowmelt (Mote *et al.* 2005; Abatzoglou *et al.* 2014; Johnstone and Mantua 2014; Jolly *et al.* 2015), increase the likelihood of larger, more severe fires. Littell *et al.* (2009) identified fuel condition (flammability) as a key driver of area burned in forests of the north-western USA and with earlier snowmelt, the flammability of subalpine parkland may increase more rapidly than at lower elevations. Previous research has shown that although temperatures increased more at higher elevations from 1991 to 2012, elevational differences were not significant for the western US as a whole (Oyler *et al.* 2015). Within our study area, maximum temperatures at higher elevations have increased more rapidly than at lower elevations in the Northern Rocky Mountains, although this pattern may reflect a bias caused by changes in how temperatures have been measured (Oyler *et al.* 2015). Three of the four ecoregions where we observed relatively higher proportions of subalpine parkland burned were in the Northern Rocky Mountains, so elevation-dependent warming may be one possible cause of the change. An assessment of whether temporal trends in the length of the fire season, fuel moisture, or 'energy release component' (Cohen and Deeming 1985) vary with elevation would help us to understand if the magnitude of climate change is greater in high- vs low-elevation vegetation types.

Climate change may also act indirectly by increasing fuel connectivity and the potential for fire to spread in the ATE. Increasing connectivity of fuels may reflect infilling of formerly open meadows by trees (Franklin *et al.* 1971; Rochefort and Peterson 1996; Miller and Halpern 1998; Schwartz *et al.* 2015) or greater mortality of trees in existing forests, thus increasing the density of standing and down fuels. Increasing connectivity of live trees is unlikely to be a major factor, however, because smaller trees are less likely to burn than larger trees in the ATE in the study region (Cansler 2015). Direct observations are needed to understand whether climate-driven increases in fuel loadings have increased the potential for fire spread, and if so, in which regions and under what climate.

The unexpected level of burning in subalpine parkland could also reflect climatically driven increases in flammability of adjacent subalpine or other forest types. In recent decades, continuous subalpine forests adjacent to parkland have burned more than other forest types. For example, from 1970 to 2003, the largest increase in frequency of large fires occurred in mid- and high-elevation forests (1680–2590 m) across the western United States and in the Northern Rocky Mountains (Westerling *et al.* 2006). Similar rapid changes in fire regime have also been observed over smaller spatial extents. Between 1984 and 2010, more subalpine forest burned than did mid-montane forest (19% vs 12%) in the Northern Rocky Mountains (data from Harvey 2015). Moreover, in two of three subalpine forest types, the mean annual area burned between 1984 and 2010 exceeded that of historical levels (Zhao *et al.* 2015). In eastern Washington, Oregon, and northern California, mortality in forest inventory plots was greatest in subalpine types and in ~30% of these plots, mortality rates were very high (≥25% per year), likely owing to fire (Reilly 2014). In the northern Cascade Range of Washington, relationships between climate and area burned and between fire severity and patch size were more pronounced in cooler and drier subalpine forests than in warmer and drier forests or cooler and wetter forests (Cansler and McKenzie 2014). Historically, fires in montane and subalpine forests have been periodic, but widespread when climate is conducive to burning (Kipfmueller 2003). Fire regimes in these forests may be more responsive to climate change because fuels are more continuous and could support extreme fire behaviour, such as crown fire and rapid fire spread (Bessie and Johnson 1995; Cansler and McKenzie 2014). Because fire is a contagious process, increasing exposure (i.e. burning in adjacent areas) should cause non-linear increases in fire in less common vegetation types (Kennedy and McKenzie 2010), such as subalpine parkland and alpine vegetation.

Increasing contagion following fire exclusion

Increasing spread of fire into the ATE may be indicative of greater-intensity fires in neighbouring lower-elevation forest – a consequence of previous fire exclusion (Hessburg *et al.* 2005, 2015; Miller and Safford 2012; Collins *et al.* 2015). The steep terrain in the Pacific Northwest and Northern Rockies places very different vegetation types in close proximity (e.g. <10 km) and these may burn in the same fires. Analyses that relate sources of ignition to spread among vegetation types or that address how probability of ignition differs from probability of burning could provide more definitive evidence that past suppression of fire at lower elevations is contributing to an increase in area burned in subalpine forests and parkland, where fires have not been actively suppressed.

Increasing wildland fire use

Changes in forest management may also have contributed to greater burning of subalpine parkland in the three Rocky Mountain ecoregions. Each of these regions has a wildland fire-use program that allows natural fires to burn. Areas in which wildland fire-use is allowed – national wilderness areas and national parks – include proportionally more subalpine and alpine vegetation than do other land designations (Scott *et al.* 2001; Dietz *et al.* 2015), making it more likely that those vegetation types will burn. Moreover, even where policy dictates that high-elevation fires should be suppressed, suppression efforts may be less aggressive than for fires in lower-elevation forest closer to human habitation.

Reduced area burned at low elevations compared with the presettlement period

Finally, recent increases in fire in subalpine parklands relative to the region as a whole may reflect that historically frequent-fire forests at lower elevations are burning less under more aggressive fire suppression. Results from the Idaho Batholith ecoregion support this idea. Here, relative to other ecoregions, fire burned larger proportions of both the subalpine and the broader landscape (reflecting a 'let-burn' policy within the Selway–Bitterroot and Frank Church–River of No Return Wildernesses; van Wagtendonk 2007). However, subalpine parkland burned less than the landscape as a whole (22% vs 29% respectively). Explicit comparisons of recent area burned with that expected under the presettlement fire regime would improve our understanding of modern fire deficits and surpluses, and how these vary among vegetation types, bringing finer resolution to studies that have examined similar questions at a regional scale (e.g. Parks *et al.* 2015).

Conclusions

More frequent fire may have positive (amplifying) or negative (stabilising) feedbacks on climate-driven changes in the ATE. Increased fire in these ecosystems could hasten climate-driven changes by removing cold-adapted and alpine species at the margins of their ranges (Lesica and McCune 2004; Gottfried *et al.* 2012), and by creating growing space that allows lower-elevation species to become established and spread. Conversely, increased fire could counteract ongoing responses to climate change, including upward movement of the treeline (Brubaker 1986; Harsch *et al.* 2009) and tree invasion of subalpine meadows (Franklin *et al.* 1971; Taylor 1995; Rochefort and Peterson 1996; Miller and Halpern 1998) by reducing tree cover and increasing the prevalence of non-forested vegetation. Fire may also interact with other stressors and disturbances to maintain existing or create new non-forested areas. For example, by changing patterns of snow deposition, fire increased tree mortality and permanently converted ribbon forest to a snow-maintained non-forested state (Billings 1969). Likewise, by removing anchor points, such as standing trees that stabilise snowpack, fire can increase the frequency and magnitude of avalanches, thus maintaining these disturbance-dependent non-forested habitats (Bebi *et al.* 2009).

Climate change will increase the prevalence of fire in western North America (Flannigan *et al.* 2006; Littell *et al.* 2010; Jolly *et al.* 2015; but see McKenzie and Littell 2016). To anticipate the consequences of climate change for subalpine parklands, additional research is needed to understand the direct effects of fire on vegetation structure and species diversity, the indirect effects on wildlife, soils and snow hydrology, and the resulting feedbacks to vegetation. For the foreseeable future, fire will remain an important disturbance process in subalpine parklands, and an infrequent, but consequential, process in alpine vegetation.

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