


Article

Post-Wildfire Regeneration in a Sky-Island Mixed-Conifer Ecosystem of the North American Great Basin

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Abstract: Information on wildfire impacts and ecosystem responses is relatively sparse in the Great Basin of North America, where subalpine ecosystems are generally dominated by five-needle pines. We analyzed existing vegetation, with an emphasis on regeneration following the year 2000 Phillips Ranch Fire, at a sky-island site in the Snake Range of eastern Nevada. Our main objective was to compare bristlecone pine (*Pinus longaeva*; PILO) post-fire establishment and survival to that of the co-occurring dominant conifers limber pine (*Pinus flexilis*; PIFL) and Engelmann spruce (*Picea engelmannii*; PIEN) in connection with site characteristics. Field data were collected in 40 circular 0.1 ha plots (17.8 m radius) randomly located using GIS so that half of them were inside (“burned”) and half were outside (“unburned”) the 2000 fire boundary. While evidence of previous burns was also found, we focused on impacts from the Phillips Ranch Fire. Mean total basal area, including live and dead stems, was not significantly different between plots inside the burn and plots outside the fire perimeter, but the live basal area was significantly less in the former than in the latter. Wildfire impacts did not limit regeneration, and indeed bristlecone seedlings and saplings were more abundant in plots inside the 2000 fire perimeter than in those outside of it. PILO regeneration, especially saplings, was more abundant than PIFL and PCEN combined, indicating that PILO can competitively regenerate under modern climatic conditions. Surviving PILO regeneration in burned plots was also taller than that of PIFL. By contrast, PCEN was nearly absent in the plots that had been impacted by fire. Additional research should explicitly address how climatic changes and disturbance processes may interact in shaping future vegetation dynamics.

Keywords: Great Basin bristlecone pine; limber pine; Engelmann spruce; Snake Range; Phillips Ranch Fire; treeline; subalpine vegetation; disturbance; Nevada; NevCAN

1. Introduction

Wildfire shapes ecosystems through multiple interacting pathways, including their species composition, nutrient cycling, and spatial structure [1,2]. As a natural agent of disturbance, fire has operated continuously during geologic eras [3,4], leaving multiple indicators of its passage and its effects upon the landscape [5]. In the western United States the role of fire varies spatially and temporally [6]. For instance, in the southwestern United States, prior to Euro-American settlement, frequent low-severity fires thinned understory vegetation in ponderosa pine forests [7], while in the upper montane and subalpine zone of the Rocky Mountains stand-replacing wildfires occurred at century-long intervals and left distinct cohorts of regeneration on the landscape [8].

Among western US ecoregions, the Great Basin stands out for its extreme topographical complexity, overall dryness, and steep orographic gradients [9], which result in sky-island montane and subalpine forests mostly dominated by conifer species [10]. Wildfire history studies in this region have focused on pinyon-juniper woodlands and mixed conifer forests [11–15]. While average fire size and total area

burned have increased in recent decades within the Great Basin [16], spatial variation in vegetation assemblages, fuel conditions, and climatic drivers has so far caused considerable variability in regional and local impacts from fire activity [17]. Long-term information on fire behavior and impacts is particularly sparse for the subalpine, sky-island ecosystems occupied by five-needle pines, e.g., limber (*Pinus flexilis* E. James) and bristlecone (*Pinus longaeva* D.K. Bailey) pine. Because the predicted increase in global fire activity [18,19] may threaten the continued presence of such high-elevation species, performing in-depth, in-situ investigations of their fire ecology in general, and of their response to wildfire in particular, can provide both scientists and land managers with valuable information.

Pinus longaeva is native to the Great Basin and typically occurs above 2500 m elevation, but is generally restricted to limestone-dolomite substrates, which are nutrient-depleted compared to other soil parent materials [20]. Current populations are considered relics of a more extensive bristlecone pine distribution during the last Glacial Maximum [21], when climate and atmospheric conditions were optimal for bristlecone physiology [22]. Shallow branching roots, waxy needles, thick cuticles, and needle retention for periods reaching 45 years [23] provide drought tolerance. Bristlecone seeds are generally wind-dispersed, and the species exhibits sufficient phenotypic plasticity to grow as krummholz above treeline, as multi-stemmed strip-bark trees in harsh xeric sites where it achieves the greatest longevity, and as upright single-bole individuals exceeding 18 m in height at more productive sites [24,25]. This phenotypic variation does not appear to be caused by genetic differences between populations [26].

Great Basin bristlecone pine is the longest-lived non-clonal organism on Earth, with individuals approaching and most likely exceeding 5000 years in age [27,28]. This iconic species has provided dendrochronologists with multi-millennial records of climatic changes [29,30], volcanic eruptions [31,32], treeline elevations [33,34], atmospheric radiocarbon [35,36], stable isotopic ratios [37,38], and archaeological environments [39]. Dendrochronologists have traditionally targeted bristlecones from marginal sites at the extremes of the species' biophysical range, where the oldest individuals with climate-sensitive growth histories can be found [40,41].

At high-elevation, cold and xeric sites, fuel loads and connectivity are low, and thus lightning-caused wildfires have been considered rare and/or limited to single-tree burning [25,42]. While natural fires are infrequent within high-elevation subalpine ecosystems [6], even bristlecone stands have fuel loads that can enable surface fire spread. Based on fire scars, Great Basin bristlecone wildfires have mean intervals between 45 and 85 years [43,44]. Fire ecology studies on the closely related Rocky Mountain bristlecone (*Pinus aristata*) have shown evidence of stand-replacing fires [45,46] as well as historical low- [47,48] and mixed-severity fire regimes [49]. *Pinus longaeva* regeneration has been examined in relation to climate and micro-site characteristics [50,51], but post-fire dynamics have received little attention, with only one study examining pre- and post-fire natural regeneration, measured four years after the 2013 Carpenter 1 Fire in the Spring Mountains of southern Nevada [52]. To expand the existing body of knowledge on fire ecology of Great Basin bristlecone pine, in this study we addressed its post-fire establishment, compared with that of co-occurring species, by examining structural conditions of a sky-island forest that burned in the year 2000. Our main objectives were (1) to examine fire effects on forest composition and structure, (2) to test whether the fire stimulated or stymied bristlecone pine regeneration, and (3) to compare *Pinus longaeva* post-fire establishment to that of other subalpine conifers, such as *Pinus flexilis* and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), in connection with site characteristics.

2. Materials and Methods

2.1. Study Area

The study area is located on Mt. Washington, in the Snake Range of eastern Nevada, between 2800 and 3500 m elevation, and centered at 38°54'54" N; 114°18'33" W (Figure 1). Mt. Washington reaches an elevation of 3553 m, and is underlain by Cambrian Pole Canyon Limestone formations [53], with soils classified as loamy-skeletal carbonatic Lithic Cryorthents [54]. Vegetation above 3000 m is dominated

by Great Basin bristlecone pine (*Pinus longaeva*: PILO), limber pine (*Pinus flexilis*: PIFL), and Engelmann spruce (*Picea engelmannii*: PCEN), while common juniper (*Juniperus communis*) is occasionally found in the understory. At elevations below 3000 m, commonly co-occurring species are white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), and aspen (*Populus tremuloides*), the only deciduous tree species in the overstory. Tree density decreases with elevation between the subalpine-montane forest transition, up to the timberline (about 3300 m) and the treeline (about 3480 m), while sporadic krummholz islands are present up to 3540 m.

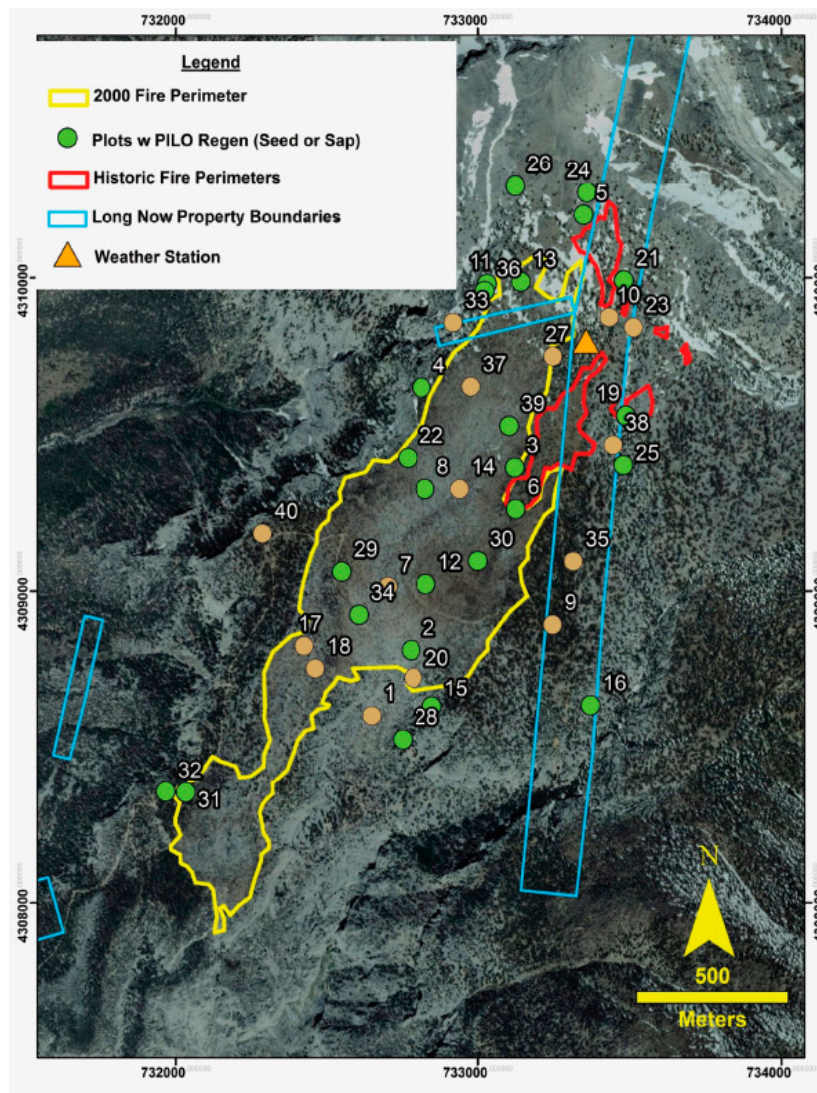


Figure 1. Map of the study area obtained from Google Earth™ imagery overlaid with the boundary of the year 2000 Phillips Ranch Fire (yellow line) and with the perimeter of older fires (red lines). Geographical coordinates are provided by the Universal Transverse Mercator (UTM) grid (zone 11 S), with tick marks and labels outside the image. The 40 randomly located plots are shown by solid green circles when they included *Pinus longaeva* (PILO) regeneration, and by solid light orange circles otherwise.

Current land ownership includes Great Basin National Park, the Long Now Foundation, and the Bureau of Land Management. Even though Mt. Washington contains the Saint Lawrence Mine, from which lead-silver ore was extracted during the early to middle 20th Century [55], no logging has occurred at the higher elevations, and the study area has been protected from human disturbance since the Park was established in 1986 [56]. Automated weather and soil sensors were installed on Mt.

Washington in 2011 as part of NevCAN, the Nevada Climate-ecohydrological Assessment Network [57]. The NevCAN station, at 3357 m elevation (Figure 1), has recorded an average total annual precipitation of 544 mm and an average annual mean air temperature of 1.4 °C. As shown by the annual cycle of precipitation and temperature (Figure S1), July is the warmest month (12.6 °C mean air temperature), and December is the coolest (−7.3 °C mean air temperature).

2.2. Field Sampling

On 15 July 2000 the Phillips Ranch Fire started in nearby Lincoln Canyon and spread up onto the southern face of Mt. Washington and the west face of Mt. Lincoln, causing high tree mortality on both mountains (Figure 1). The fire perimeter was mapped using both remote sensing and ground surveying. Three forms of imagery from years as close to the 2000 fire as possible were used to identify burned areas: false color composites of Landsat 7 ETM+, burned area maps from Monitoring Trends in Burn Severity [MTBS]; [58], and Google EarthTM imagery. Fire boundary perimeters were mapped both using imagery and from in situ reconnaissance during May 2012. During ground-truthing, fire-scarred bristlecone pines were also located and mapped.

Forty circular 0.1 ha plots (17.8 m radius) were randomly located using GIS so that half of them were inside (“burned”) and half were outside (“unburned”) the fire boundary within the subalpine vegetation zone. Maximal distance from the fire boundary was constrained by physiographic breaks in ecosystem features such as cliffs to the west and south, a valley to the east, and the treeline to the north. At each plot all stems (seedlings, saplings, trees, logs, and snags) were measured and mapped during the summer of 2012 and 2013 (Table S1). Mapping was done using polar coordinates relative to the plot center. To minimize transcription and omission errors, all field data were digitally recorded using a task-specific dictionary on a Trimble Nomad hand-held computer. Seedlings were stems ≤ 30 cm in height, saplings were >30 cm and ≤ 3 m in height and less than 5 cm in diameter at breast height (DBH), and trees were taller or larger than saplings. Logs were dead and down trees, while snags were standing dead trees. Regeneration was quantified by combining seedlings and saplings, and assuming that they regenerated post-fire, i.e., they were less than 13 years old. Evidence of past fire, besides charred snags, logs, and stumps, included damage to live stems, such as char and fire scars. Tree condition (size, vigor, crown and/or stem damage) was assessed to determine whether the fire evidence was for a recent (year 2000) or previous event.

2.3. Data Analysis

Differences between various metrics of vegetation structure and tree morphology in burned and unburned plots were initially evaluated using two-sample t-tests. Abundance of seedlings, saplings, and their sum, i.e., total regeneration, was then compared between plots within (“burned”) and outside (“unburned”) the fire perimeter for each species (PILO, PIFL, and PCEN) and for the three conifers combined using Generalized Linear Models (GLM) with a negative binomial error distribution calculated by the MASS package in the R software environment [59]. Regeneration was examined with regard to plot features measured in the field (Table S1) as well as plot topographic characteristic from GIS layers, calculated in the laboratory. Spatial predictors included plot distance to the fire edge, terrain ruggedness [60], and three remotely sensed indices, the normalized difference vegetation index [NDVI] [61,62], the normalized burn ratio [NBR] [63], and the normalized difference moisture index [NDMI] [64]. These three indices were obtained from Landsat Climate Data Record surface reflectance imagery [65] via the USGS Earth Explorer data portal. The best predictive model of regeneration was selected using the Bayesian Information Criterion [BIC] [66], a metric that minimizes deviance while penalizing each additional predictor variable, thus encouraging model parsimony [67].

To assess density differences amongst species (PILO, PIFL, and PCEN), burn status, and size classes, contingency tables were constructed using the cumulative counts from plots within and outside the fire perimeter. Contingency tables were compared using the odds ratio, which divides the proportion of one column by the proportion of the other column [68]. To aid interpretation,

the columns in the division were ordered so that the odds ratio was always ≥ 1 [68]. If all cell counts in a contingency table were greater than five, significance was determined using the Chi-squared test of independence, otherwise Fisher's exact test with midpoint correction was used [69]. These analyses were performed using the *epitools* R software package [70]. The first contingency table compared abundances of regeneration (seedlings and saplings) between burned and unburned plots by species. The second comparison was focused on seedlings alone, and how they varied by species for burned and unburned plots, to detect differences in more recent regeneration. The third comparison focused on recent post-fire regeneration (i.e., seedlings in burned plots) as they related to tree abundances by species, which represented stand composition and potential seed sources.

3. Results

3.1. Fire Mapping

Based on remotely sensed images and indices, as well as on field reconnaissance mapping, the 2000 Phillips Ranch fire spread over approximately 83 ha on Mt. Washington (Figure 1). Boundaries between unburned areas and areas of high-severity burning were recognizable both from the aerial imagery and during field work, with small zones of mixed-severity fire containing surviving trees that exhibited direct fire effects such as stem char, fire scars, or partially consumed canopies. Outside of the 2000 fire perimeter, a total of 62 fire scars were observed on *Pinus longaeva* trees, suggesting that low-severity fires had occurred in bristlecone pine habitat prior to the year 2000. Fire scars were also observed on dead trees within the burned area, and such scars must have predated the 2000 fire.

Remote sensing imagery and field reconnaissance confirmed the presence of an area adjacent to the boundary of the 2000 fire that was occupied by fire-killed trees but constituted an older, high-severity, burned patch (Figure 2). Live saplings and small trees were present at the time of our sampling inside this area, whereas burned snags were lacking both branches and bark. This burned patch is visible in 1945 aerial imagery, thus indicating that the fire occurred prior to 1945, and possibly at the turn of the 20th Century given the presence of bristlecone saplings and small trees.

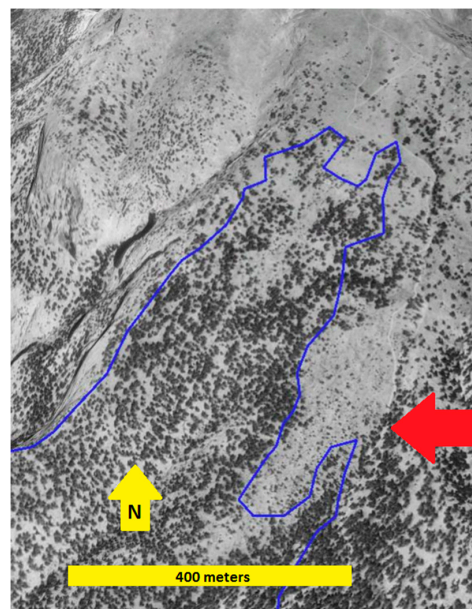


Figure 2. Remote sensing imagery of Mt. Washington in the 1990s, prior to the 2000 fire (blue line). A previously cleared forest section (red arrow) showed on-the-ground evidence of wildfire-killed trees.

3.2. Vegetation Analysis

The 40 sampled plots were located on terrain with widely different slopes (mean of 28%, standard deviation of 16%), ranging from almost flat (5%) to extremely steep (70%). Elevation varied between 2910 and 3460 m (mean of 3207 m, standard deviation of 147 m). Exposures ranged clockwise from roughly east (70°) to roughly west (290°), hence they did not include northerly aspects. Since exposure was measured in degrees, it was summarized using circular statistics [71], giving an average of 200°. It was noted during field work that regeneration seemed more abundant at higher elevations, i.e., near treeline. However, of the nine plots above 3350 m elevation, only one showed evidence of the 2000 fire.

Overall, the plots represented a range of post-fire conditions, from areas of complete tree mortality caused by the fire, where stems were mostly snags, to areas outside the burn, where mortality was minimal (Figures 3 and 4). Fewer live trees (378) were recorded on the 40 plots compared to dead ones (419 snags and 109 logs). Total stem density, including both live and dead trees, was not statistically different between plots located within the fire and those outside the burn perimeter (Table 1). Some mortality was observed in unburned areas, but reduced by a factor of 10, as shown by the percentages of tree stems that were snags: $87.4 \pm 4.2\%$ within the burn, and $8.5 \pm 2.0\%$ in unburned areas. Snags were bigger and taller in plots within the fire than in plots outside its boundary (Table 1), possibly because of the near-complete mortality, including the largest trees, inside the fire, whereas mortality in areas outside the fire could involve smaller trees because of competitive interactions. Mean total basal area was not significantly different between plots inside the burn ($24.8 \pm 2.1 \text{ m}^2 \text{ ha}^{-1}$) and plots outside the fire perimeter ($25.1 \pm 4.7 \text{ m}^2 \text{ ha}^{-1}$), but live basal area was significantly less in the former ($3.3 \pm 1.7 \text{ m}^2 \text{ ha}^{-1}$) than in the latter ($23.1 \pm 4.6 \text{ m}^2 \text{ ha}^{-1}$). Plots within the fire perimeter included surviving trees only if located near the burn periphery (plots 28, 31, and 40; Figure 1).

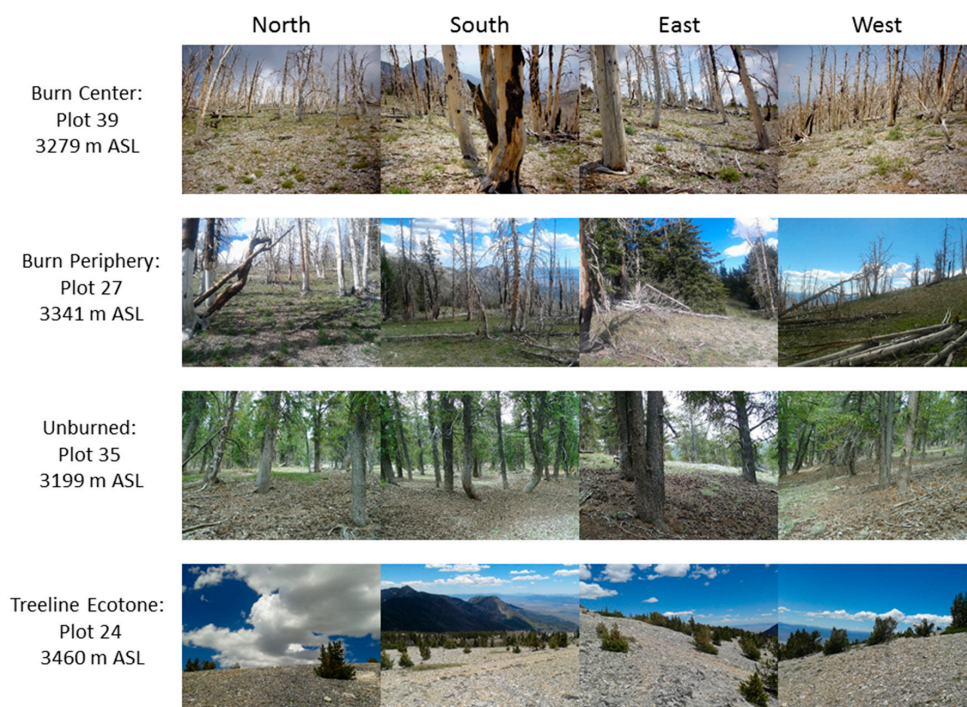


Figure 3. Photographs of four plots sampled during the 2012 and 2013 field seasons (see Figure 1 for plot locations). One photograph was taken for each cardinal direction (photo credits: M. Kilpatrick). The plots represent features of the study area (from top to bottom): center of the area burned in year 2000, edge of the burned area, outside the burned area, and near treeline (i.e., elevation ≥ 3350 m). All stems mapped at these plots were *Pinus longaeva* and *Pinus flexilis* (Figure 4).

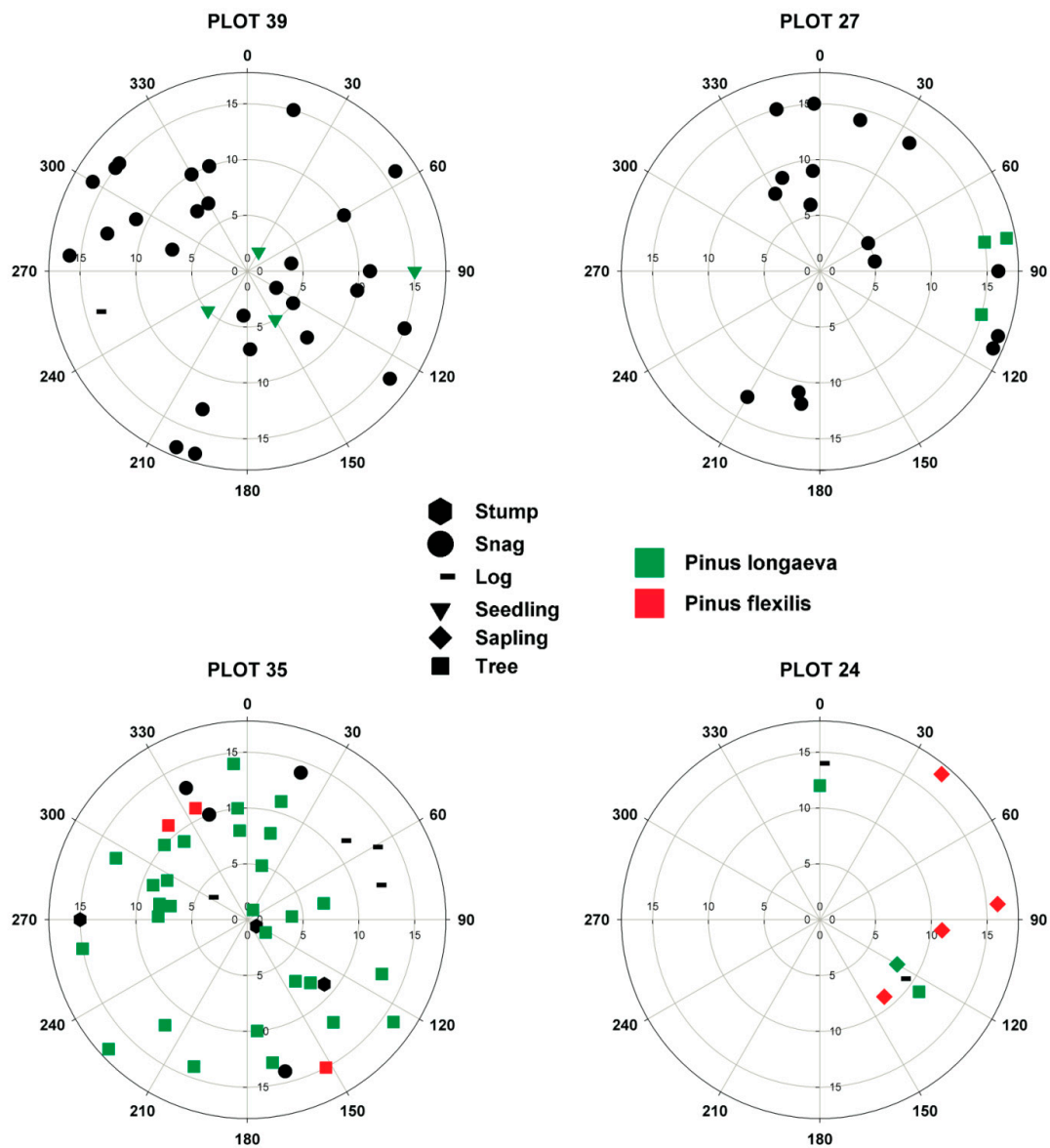


Figure 4. Maps of the four plots whose photographs (Figure 3) were used to represent field conditions. Colors were used to identify species, and solid symbols were used to represent dead (Stump, Snag, Log) and live (Seedling, Sapling, Tree) stems.

Table 1. Characteristics (mean \pm standard error) of sampling plots inside (“Burned”) and outside (“Unburned”) the 2000 fire perimeter.

Vegetation Feature	Unburned Plots	Burned Plots	% Change ¹	<i>p</i> -Value ²
Total Tree Stems ($n \text{ ha}^{-1}$)	215 \pm 23	202 \pm 16	−6	0.75
Live Trees ($n \text{ ha}^{-1}$)	197 \pm 33	27 \pm 10	−86	<0.001
Snags ($n \text{ ha}^{-1}$)	18 \pm 4	175 \pm 20	872	<0.001
Total Tree Basal Area ($\text{m}^2 \text{ ha}^{-1}$)	25 \pm 5	25 \pm 2	0	0.94
Live Tree Basal Area ($\text{m}^2 \text{ ha}^{-1}$)	23 \pm 5	3 \pm 2	−87	<0.001
Snag Basal Area ($\text{m}^2 \text{ ha}^{-1}$)	2 \pm 0.4	22 \pm 2	1000	<0.001
Live Tree Height (m)	7 \pm 1	8 \pm 2	14	0.74
Snag Height (m)	6 \pm 1	10 \pm 1	67	0.01
Live Tree Diameter (cm)	36 \pm 4	38 \pm 15	6	0.95
Snag Diameter (cm)	28 \pm 6	41 \pm 2	46	0.03

¹ Difference between the mean of burned and unburned plots, divided by the unburned plots mean. ² Based on a two-sample *t*-test; values <0.05 were highlighted using italic font.

Live vegetation was dominated by *Pinus longaeva* (70.4% of all recorded trees), followed by *Picea engelmannii* (19.3%) and *Pinus flexilis* (9.0%); other species (*Abies concolor*, *Populus tremuloides*, and *Pseudotsuga menziesii*) accounted for <1% each of all recorded trees. Regeneration of subalpine species (PILO, PIFL, and PCEN; Table 2), given by the combined abundance of seedlings and saplings on all 40 plots, was a total of 188 stems, equivalent to 47 ± 9.8 stems ha^{-1} . *Pinus longaeva* dominated the regeneration counts, with 109 stems (57% of total), more than twice the regeneration of *Pinus flexilis* (51 stems, 35% of total), which was slightly less than double the *Picea engelmannii* regeneration (28 stems, 7% of total). Regeneration of other tree species summed to 30 stems, most of which were found on plot 31 (Figure 1), the fourth lowest in elevation (2991 m). Unburned plots near treeline (i.e., at elevations ≥ 3350 m) had lower tree density (mean of 145 trees ha^{-1}) than unburned plots at lower elevations (mean of 237 trees ha^{-1}), but were characterized by greater regeneration abundance (odds ratio: 1.64, p -value = 0.02).

Table 2. Summary of regeneration counts (i.e., total seedlings and saplings) for plots inside (“Burned”) and outside (“Unburned”) the 2000 fire perimeter.

Variable	ALL ¹		<i>Pinus longaeva</i>		<i>Pinus flexilis</i>		<i>Picea engelmannii</i>	
	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned
Mean	5.9	5.1	3.0	2.5	1.6	0.7	0.2	1.7
Stand. Dev.	11.8	5.1	5.1	3.9	2.7	1.5	0.4	2.7
Median	2.0	3.5	1.0	1.0	0.0	0.0	0.0	0.5
Minimum	0	0	0	0	0	0	0	0
Maximum	55	17	22	16	8	6	1	10
No regeneration (% plots)	18	17	36	33	64	72	82	50
Total Seedlings	63	33	32	23	28	6	3	4
Total Saplings	41	51	33	21	7	10	1	20

¹ ALL = *Pinus longaeva* + *Pinus flexilis* + *Picea engelmannii*.

3.3. Regeneration Analysis

The PILO and PIFL mean plot regeneration was greater within the fire perimeter (“burned”, Table 2 and Table S2). PCEN displayed the opposite pattern, with significantly more abundant saplings in “unburned” plots than “burned” ones (Table 2 and Table S2). More PIFL seedlings were recorded in plots within the fire perimeter than in those outside of it (Table 2 and Table S2). The same pattern, albeit less pronounced, was found for PILO, whereas PCEN seedlings were about the same in “burned” and “unburned” plots (Table 2 and Table S2). When only “burned” plots were considered, PIFL had significantly more seedlings relative to same-plot tree abundances (28 to 35) than PILO (32 to 268), while PCEN had the lowest seedling-to-tree ratio (3 to 75). These results indicate that PIFL has been spreading in the “burned” sites compared to the other two species, even though PILO regeneration (seedlings and/or saplings) was the highest in both “burned” and “unburned” plots (Table 2).

Seedlings to saplings proportions were significantly greater at “burned” than “unburned” plots for PIFL (odds ratio 6.3; p -value = 0.002), less so for PCEN (odds ratio 12.2; p -value = 0.04), and not significantly different for PILO (odds ratio 1.1; p -value = 0.76). The size distribution of surviving regeneration (Figure 5A) was significantly different (chi-square p -value < 0.001) between plots inside the fire perimeter (“burned”) and those outside (“unburned”). In plots that were not affected by the fire, regeneration showed a slightly bimodal distribution with a peak in the smallest size classes, i.e., <60-cm height, and another one between 1.2 and 1.8 m in height. In plots that had been impacted by the fire, regeneration was mostly <1 m in height. In “burned” plots, only 1/6th of stems were >60 cm in height, half of which were in plot 31 near the montane-subalpine transition (Figure 1).

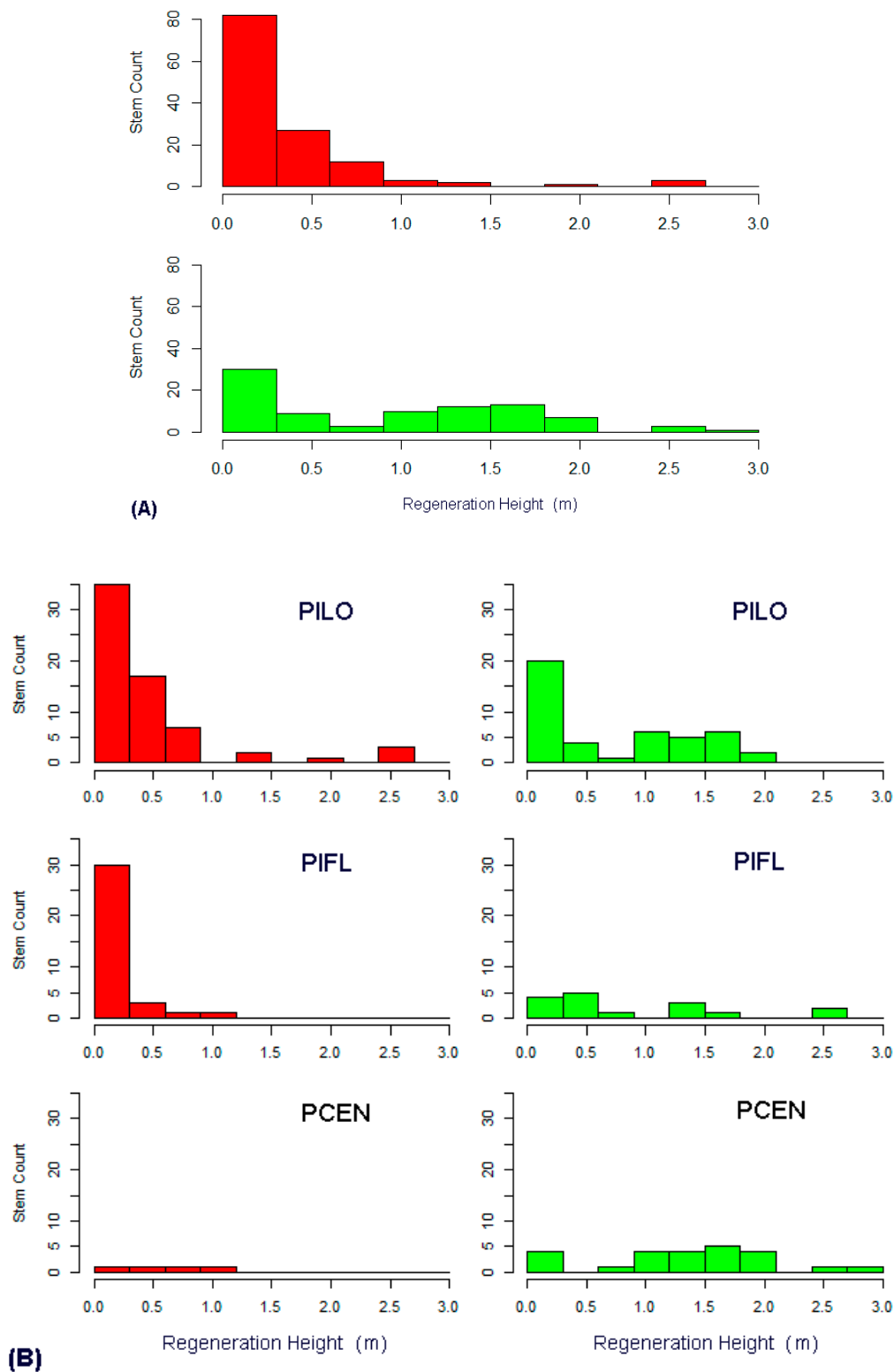


Figure 5. Histograms of regeneration size based on 30-cm height classes for plots inside the fire parameter (“burned”, red bars) and outside of it (“unburned”, green bars). The smallest size class, 30 cm or less, identifies seedlings, while the remaining size classes, up to 3 m, represent saplings. (A) All species combined. (B) Species-specific histograms: PILO = *Pinus longaeva*; PIFL = *Pinus flexilis*; PCEN = *Picea engelmannii*.

Regeneration of bristlecone pine (PILO) had a mean height (0.50 ± 0.07 m) significantly greater (p -value < 0.001) than limber pine (PIFL) regeneration (0.23 ± 0.03 m). PILO had also greater abundance of saplings than PIFL, for which regeneration was almost entirely restricted to seedlings (Figure 5B). These differences may indicate that PILO recolonized burned areas more rapidly than PIFL, or that PILO grew more rapidly than PIFL, or that PIFL regeneration was more recent than the PILO one. By contrast, PCEN was nearly absent in the plots that had been impacted by fire. Seedlings were rare overall for PCEN, whereas saplings were present in plots outside the fire perimeter (Figure 5B). At elevations above 3350 m, PCEN occurred almost exclusively in ribbon-type clusters most likely derived from vegetative reproduction, whereas at lower elevations only the single-bole growth form occurred, indicating regeneration from seeds.

In general, regeneration was lowest near the center of the fire, where distances to seed source were the greatest. Indeed, regeneration was not homogeneously distributed throughout the study area, with seedlings absent from 17 (6 burned, 11 unburned) of the 40 plots, while both seedlings and saplings were absent from 8 plots. With regard to plot features connected with seedling abundance, the BIC-selected models explained relatively small amounts of variability, and only the model for PILO had significant coefficients (Table S3), two of them (for maximum tree height and for distance to the fire perimeter) negative, and the other two (for number of snags and for terrain ruggedness) positive.

4. Discussion

More than one high-severity fire occurred at the study area, indicating that the 2000 Phillips Ranch Fire was not a unique event, and that such fires may be part of the natural range of variation in bristlecone pine stands. In a 1988 scientific article about bristlecone pine regeneration [72], a photo published as Figure 1 shows “fire-killed” *Pinus longaeva* trees on Mt. Washington that are identical to the snags that resulted from the 2000 fire. Additionally, the presence of fire scars, sometimes multiple scars per tree, on live PILO outside the 2000 fire perimeter, and on dead snags within the fire perimeter, suggests spatial concurrence of high- and low-severity fires, although most likely occurring at separate times. Fire-scarred bristlecone pines were all single-stem trees with an upright growth form, perhaps an indication that PILO vulnerability to fire may be related to morphology, with multi-stemmed trees more likely to be killed than scarred by fire. Slow-growing PILO is characterized by extreme longevity with regard to cell senescence, reproduction, growth, and physiology [73–76], with disturbances such as soil erosion or mechanical damage contributing to the demise of individual trees. While lightning strikes or subsequent spotty, low-severity fires may cause isolated mortality in most bristlecone pine stands, such events would be unlikely to act as agents of natural selection, so that multi-stemmed growth forms would not be penalized in terms of fitness, and in fact genetic variation amongst bristlecone pine sites is negligible [26].

Similar total stem density, total basal area, mean stem height, and mean stem diameter suggest that areas impacted by the 2000 fire were structurally similar, in terms of vegetation, to those that did not burn. Differences in post-fire stand structure and regeneration are therefore unlikely to be artifacts of pre-fire differences. Our results indicate that wildfire impacts did not limit PILO regeneration, and indeed bristlecone seedlings and saplings were more abundant in plots inside the fire perimeter than in those outside of it, but not to a statistically significant level.

Sapling abundance was lower in plots that had been impacted by the 2000 fire, but mostly because of differences related to PIFL and, even more so, PCEN. It should be emphasized that saplings located inside the fire perimeter could not have predated the 2000 fire because complete mortality of large and small trees within the burned area, i.e., extreme fire severity, was observed both in the field and from remote sensing datasets. In addition, surface-level charring was present on snags, indicating surface spread along with crown fire conditions. In situ photographs (e.g., Figure 3) illustrate conditions at the time of sampling, and comparing burned with unburned areas supports the notion that sapling-sized stems were extremely unlikely to have survived the fire.

PILO regeneration, especially saplings, was more abundant than PIFL and PCEN combined, indicating that PILO can competitively regenerate following wildfire under current climatic conditions. Surviving PILO regeneration in burned plots was also taller than that of PIFL. It is possible that PILO seedlings grow faster on limestone derived soils because PILO can withstand the exacerbated moisture stress caused by N and K depletion on such substrates [77]. A high-severity fire should cause organic layer consumption because of high surface heating, creating an environment where moisture-use efficiency is critical. It has been shown that PILO is characterized by tracheids with smaller lumen area than either PIFL or PCEN [78], and thus can tolerate higher internal water stress. PCEN was the least adept at establishing in burned areas, most likely because its seedlings do not tolerate high sun exposure and the associated moisture stress [79,80], while partial shading by herbaceous or woody species enhances PCEN seedling survival at high elevations [81,82]. Near treeline PCEN formed ribbon forest bands, which are considered to derive from vegetative reproduction and may allow PCEN persistence at the highest elevations because inter-stem proximity reduces abiotic stresses, such as drought, sun-exposure, and ice-crystal abrasion [83,84].

Seedling proportions were significantly greater in burned plots only for PIFL, suggesting that limber pine is an apt post-fire colonist in the Great Basin. In fact, PIFL seedlings were nearly exclusive to burned areas, whereas PILO seedlings were found in both burned and unburned plots. Moreover, because seedlings to saplings proportions were significantly greater at “burned” than “unburned” plots for PIFL but not significantly different for PILO, it is plausible that PILO was initially more successful than PIFL in reoccupying the site, whereas in recent years the opposite pattern is taking place. Additional evidence for limber pine recently “leap-frogging” over bristlecone pine at high elevations in the Great Basin has been gathered by looking at treeline advances in the absence of recent fires [85]. Successful post-disturbance regeneration of limber pine in the Rocky Mountains has been linked with caching by the Clark’s nutcracker (*Columbiana nucifraga*) [46,86]. A similar dispersal mechanism has been proposed for bristlecone pine in the Great Basin [72], mostly because of the presence of clumped and multi-stemmed trees. However, this hypothesis was not supported by allozyme data from 210 bristlecones in three groves of the White Mountains [87].

Vegetation features influenced by wildfire can create site conditions conducive to PILO regeneration. For instance, at the plot level, snag abundance positively influenced PILO seedling abundance (Table S3), and because snags were most common in burned plots this suggests an indirect link between regeneration and wildfire. Snags do not compete for water and nutrients, and could provide some protection from moisture stress and desiccation during the early stages of seedling growth. Ground cover conditions, including the location and amount of deadwood, can produce microsite features that enhance establishment of regeneration [88,89]. Seedlings of multiple woody species grew and survived better when planted under the canopy of existing shrub species, especially in dry environments [90]. The distance to burned edge was inversely correlated with seedling abundance of both PILO and PIFL (Table S3), meaning that regeneration was more abundant closer to the fire perimeter, where distances to live seed sources were lower. This relationship would then be consistent with wind-driven seed dispersal.

The inverse relationship between maximum tree height and PILO regeneration (Table S3) was likely connected with increased competition for light, water, and nutrients caused by taller live individuals. For PIFL, distance to the burn edge was a significant inverse predictor of regeneration; as for PILO, however, the coefficient was an order of magnitude lower (Table S3), possibly because of greater bird dispersal [86]. Generally, PILO and PIFL seedlings favored similar sites, namely those with low canopy cover, proximate to the fire edge, hence to seed sources, and on more complex terrain where moisture retention may be enhanced by concave features. These findings differ from results obtained in the White Mountains, where shade and low temperatures were found to favor PILO seedling survival [50]. While we can hypothesize that such differences are related to post-fire ecosystem dynamics, further research is needed to disentangle the underlying mechanisms.

Live tree basal area in plots within the fire perimeter was only 14% of what it was in plots outside the fire (Table 1). Given that total stem density, total basal area, mean stem height, and mean stem diameter were similar between burned and unburned areas, and that decomposition processes are relatively slow in these dry and cold sky-island environments [91], one could infer, as noted earlier, that vegetation structure prior to the 2000 fire was relatively homogeneous across the entire study area. Therefore, post-fire recovery at this site has clearly been slower than in other, moister subalpine forests. As an example, the Yellowstone fires of 1988 were followed by regeneration densities often 10 to 100 times greater than pre-fire densities [92], especially in stands dominated by lodgepole pine (*Pinus contorta*). In the southern Rocky Mountains, 29 years after burning, regeneration densities for *Pinus aristata*, *Pinus flexilis* and *Picea engelmannii* were considerably higher than at our study area, with spruce establishment considerably more successful than for pines [46]. Sparse *Pinus longaeva* regeneration was found four years after a high-severity fire in the Spring Mountains of southern Nevada [52], and overall one may infer that in Great Basin sky-island ecosystems the regeneration response subsequent to burning is relatively slow.

Plots at higher elevations showed greater regeneration as well as lower stem densities, tree heights, and basal area, corresponding to open canopies and abundant solar radiation, which are favorable to PILO and PIFL regeneration. Bristlecone establishment and survival is episodic [24] and inextricably linked to favorable climatic periods [51], and thus the enhanced regeneration observed at higher elevations in the absence of fire points to recently favorable climatic conditions. Proxy climate records and long records of tree growth from the Snake Range indeed suggest warming air temperatures in recent decades [93,94]. Seedlings typically possess a narrower range of climatic tolerance than adults [95,96] and are thus more vulnerable to a variety of stressors including drought, frost damage, desiccation, overheating, and poor carbon acquisition. It is then well known that establishment and survival of seedlings presents the greatest barrier to range expansions. On the other hand, seedling establishment represents only the first step in the process of post-fire stand recovery, and as such it is not sufficient to predict future survivorship that could lead to stand composition changes.

5. Conclusions

Post-fire stand recovery in a sky-island ecosystem of the Great Basin dominated by five-needle pines occurred slowly but successfully. Wildfire impacts did not limit regeneration, and indeed bristlecone seedlings and saplings that were alive 12 years after the 2000 fire were more abundant in plots inside the fire perimeter than in those outside of it, but not to a statistically significant level. PILO regeneration, especially saplings, was more abundant than PIFL and PCEN combined, indicating that PILO can competitively regenerate under current climatic conditions. Surviving PILO regeneration in burned plots was also taller than that of PIFL. By contrast, PCEN was nearly absent in the plots that had been impacted by fire. Given the size and abundance of regeneration both inside and outside the burn perimeter, it is plausible that PILO was initially more successful than PIFL in reoccupying the site, whereas in recent years, the opposite pattern has been taking place. Additional research should explicitly address how climatic changes and disturbance processes may interact in shaping future vegetation dynamics in these iconic mountain environments.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1999-4907/11/9/900/s1>. Figure S1: Walter–Lieth diagram of average monthly mean temperature (red line) and average monthly total precipitation (blue line) from the NevCAN station during 2011–2017 (see text for details). Bars on the x-axis indicate frost season (dark blue), probable frost season (light blue), and frost-free season (no bars). Moisture surplus (area with blue vertical lines) occurs most of the year because of the relatively high elevation (3357 m) of the site. Moisture deficit (area with red dots) occurs only in June. Table S1: Summary of data collected in the field using a predefined “dictionary”, i.e., a list of variables, measurement units, and predetermined choices, on a Trimble Nomad hand-held computer. Table S2: Comparison of regeneration abundances (i.e., number of seedlings and saplings) in plots within the 2000 fire perimeter (“Burned”) and in plots outside that boundary (“Unburned”; see text for details). Table S3: Summary of regression models used to evaluate plot features connected with seedling abundance.

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