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Regeneration of Rocky Mountain bristlecone pine (*Pinus aristata*) and limber pine (*Pinus flexilis*) three decades after stand-replacing fires[☆]

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A B S T R A C T

Rocky Mountain bristlecone pine (*Pinus aristata*) and limber pine (*Pinus flexilis*) are important high-elevation pines of the southern Rockies that are forecast to decline due to the recent spread of white pine blister rust (*Cronartium ribicola*) into this region. Proactive management strategies to promote the evolution of rust resistance and maintain ecosystem function require an improved understanding of the role of disturbance on the population dynamics of both species and environmental conditions that favor seedling establishment. We examined patterns of bristlecone and limber pine regeneration across the perimeters of three, 29-year-old, high-severity burns in northern, central, and southern Colorado: Ouzel, Badger Mountain, and Maes Creek, respectively. Both species exhibited a very protracted regeneration response to these fires. Bristlecone pine regeneration was concentrated near burn edges and beneath surviving seed sources. This spatial pattern is consistent with limitations incurred by wind-dispersal, also borne out by the low occurrence of seedling clusters. Relative to unburned stands, the absolute abundance of bristlecone pine generally increased only on plots retaining some surviving trees. Limber pine regeneration pattern varied between sites: high in the burn interior at Ouzel, concentrated at burn edges at Badger, and mostly in unburned stands at Maes. Clark's Nutcracker dispersal of limber pine in each study area was indicated by high seedling distance from possible seed sources and high frequencies of clustered stems. Except at Ouzel, the absolute abundance of limber pine decreased in burns. Across sites, establishment by both species was boosted by nearby nurse objects (rocks, fallen logs, and standing tree trunks), a relationship that extended out at least as far as the closest three such objects, usually found within 50 cm. Fire decreased the frequency of *Pedicularis* but increased *Castilleja* and *Ribes* species (alternate hosts of white pine blister rust), though only one species, *R. cereum*, was positively associated with either pine species. We conclude that regeneration of bristlecone and limber pine may benefit from natural disturbance or proactive management creating appropriately sized openings and microtopographic structure (e.g., abundant fallen logs); however, beneficial responses may require many decades to be achieved.

1. Introduction

Rocky Mountain bristlecone pine (*Pinus aristata* Engelm) and limber pine (*Pinus flexilis* James) are important high-elevation five-needle pines of the southern Rocky Mountains. At present, both species—and the biological communities they form—are forecast to decline extensively due to the recent and rapid spread of white pine blister rust (*Cronartium ribicola* J.C. Fisch.) in Colorado (Schoettle, 2004; Howell et al., 2006). Both five-needle pines can occur at the environmental margins of the tree life form: at alpine treelines, on windswept ridges, and on dry, rocky, south-facing slopes (Peet, 1978; Veblen, 1986; Baker, 1992), where they are known for their extreme longevity (>1500 years; Brunstein and Yamaguchi, 1992; Schuster et al., 1995) and the aesthetic growth forms such long-lived trees can take in these settings. Both species may also form extensive, closed-canopy forests in more productive settings (Schoettle, 2004). Where they occupy environments near or beyond the physiological tolerances of other tree species, they provide irreplaceable wildlife habitat and ecosystem services (Schoettle, 2004). However, key aspects of the ecology of both species remain poorly understood—an understanding upon which

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effective management for blister rust will depend (Schoettle, 2004; Schoettle and Sniezko, 2007).

In Colorado, Rocky Mountain bristlecone pine (henceforth, bristlecone pine) and limber pine exhibit a latitudinal and elevational shift in dominance (Peet, 1978). In northern Colorado, beyond the northern range limit of bristlecone pine, limber pine is frequently dominant in dry subalpine forests, though it also occupies xeric sites across the elevational gradient from lower- to upper-treeline (Peet, 1978; Schoettle and Rochelle, 2000). Farther south, where ranges of bristlecone and limber pine overlap, bristlecone pine usually dominates the highest elevations, and limber pine is restricted to lower sites, though bristlecone pine may also assume dominance across a broad elevational gradient (Peet, 1978) in the core of its geographic range.

Across their ranges, bristlecone and limber pine may experience a large variety of fire regimes. In open stands on rocky, unproductive sites where fuels are limiting, fire is rare and unimportant. In contrast, on more productive sites, both bristlecone and limber pine appear to be largely dependent on infrequent, stand-replacing fire to reduce competition by other tree species and create open conditions that promote regeneration. In the northern Front Range of Colorado, limber pine is often the first tree species to colonize large, high-elevation, stand-replacing burns, and is gradually replaced by more shade-tolerant spruce and fir (Veblen, 1986; Rebertus et al., 1991; Donnegan and Rebertus, 1999), suggesting that its long-term persistence in the subalpine landscape is dependent on high-severity wildfire. Likewise, based on a survey of 65 sites across Colorado, Baker (1992) concluded that bristlecone pine principally established following high-severity fire, and was gradually succeeded by spruce in the absence of fire. However, fire history reconstructions have indicated that in some locations at least, both limber pine (Sherriff et al., 2001) and bristlecone pine (Donnegan et al., 2001; Brown and Schoettle, 2008) experienced more frequent, but non-lethal fires.

Differences between bristlecone and limber pine in post-fire regeneration are not known, but would be expected based on different mechanisms of seed dispersal. The large (ca. 100 mg), wingless seeds of limber pine are dispersed primarily by Clark's nutcrackers (*Nucifraga columbiana* Wilson; Woodmansee, 1977; Lanner and Vander Wall, 1980). Nutcracker-dispersed seeds are often carried distances >100–1000 m, and are directed into open sites such as the exposed interiors of large burns (Tomback, 2001 and references cited therein). Because nutcrackers often deposit numerous seeds in each cache, limber pine seedlings arising from caches often occur in clusters of multiple individuals (Woodmansee, 1977; Lanner and Vander Wall, 1980; Carsey and Tomback, 1994). Bristlecone pine seeds are small (ca. 20 mg) and winged, typical of wind-dispersal. Similar wind-dispersed pine seeds typically follow an exponential decay function, with most seeds retained within 10–100 m of the parent tree (McCaughey et al., 1986). However, the closely related Great Basin bristlecone pine (*Pinus longaeva* D.K. Bailey), which also produces small, winged seeds, may in fact be nutcracker-dispersed, as reported by Lanner (1988) based on the frequency of stem clusters and observations of nutcrackers.

Both bristlecone and limber pine are highly susceptible to white pine blister rust (Hoff et al., 1980), a fungal pathogen with a complex life cycle requiring five-needle pines of subgenus *Strobus*, and alternate host species of *Ribes*, *Castilleja*, or *Pedicularis* (McDonald et al., 2006). Endemic to high-latitude and high-elevation Asian white pines, white pine blister rust was inadvertently introduced to North America at the beginning of the 20th century, and its effects have been dramatic. Among stands of high-elevation whitebark pine (*Pinus albicaulis* Doug. ex Hook.) and limber pine in the northern Rockies of Montana, Idaho, and Wyoming, blister rust has often resulted in >90% mortality (Kendall and Kearne, 2001), driving major shifts in the composition, structure, diversity, and functioning of these ecosystems (Tomback and Kendall, 2001). In the southern Rockies, white pine blister rust is of very recent origin, first encountered in limber pine in Colorado in 1998 (Johnson and Jacobi, 2000) and in bristlecone pine in 2003 (Blodgett and Sullivan, 2004). However, climatic conditions favor continued pathogen expansion throughout the southern Rockies (Howell et al., 2006), and blister rust is expected to exert major negative impacts on five-needle pines across the region (Schoettle, 2004).

To promote the evolution of rust resistance and to maintain functioning of five-needle pine ecosystems, Schoettle and Sniezko (2007) proposed proactive land management strategies that include the outplanting of rust-resistant seedlings and silvicultural treatments that increase natural establishment before pathogen invasion. Both approaches require an improved understanding of five-needle pine seedling ecology, particularly how canopy cover, herb and shrub communities, microtopographic structure, and ground cover affect establishment. Canopy shade may inhibit seedling establishment but at high elevations may also protect seedlings from excessive solar radiation and nighttime heat loss via long-wave reradiation (Germino and Smith, 1999). Likewise, understory plant cover may exert negative or positive effects: dense herb competition can prevent post-fire tree establishment (Stahelin, 1943); however, neighboring plants may also ameliorate extreme conditions and facilitate tree seedling establishment in subalpine environments (Maher et al., 2005). Shelter by microtopographic features such as fallen logs (Lampainen et al., 2004) or boulders (Resler et al., 2005) may also promote tree seedling establishment. Lastly, depending on the effects of fire on bristlecone and limber pine populations, prescribed fire and/or wildfire management may benefit both species. However, fire may also create habitat for shade-intolerant *Ribes* spp. (Marshall, 1995) or other alternate hosts of white pine blister rust, potentially amplifying pathogen exposure.

The purpose of this research is to assess patterns of bristlecone and limber pine regeneration at three ca. 30-year-old, high-elevation, high-severity burns in Colorado (Fig. 1) to provide insight into: (1) general effects of fire on five-needle pine regeneration (i.e., three decades after fire, did burning increase the abundance of either species on the landscape?), (2) differences between bristlecone and limber pine post-fire establishment

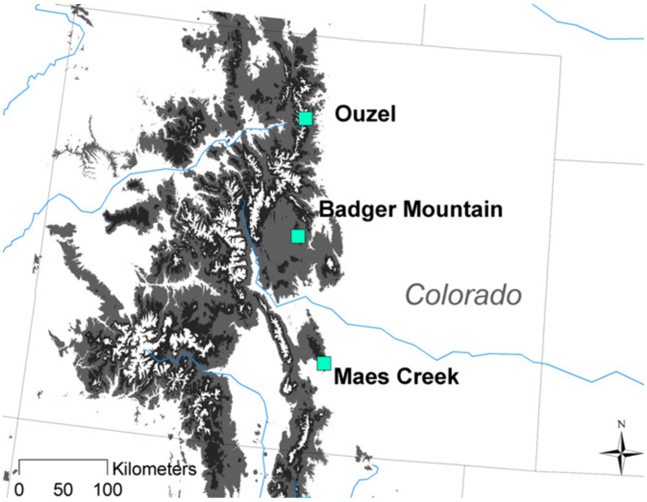

Fig. 1. Locations of study sites in Colorado.

pattern that may be related to seed dispersal, (3) microsite conditions that promote or hinder seedling establishment, including canopy cover, understory vegetation, ground cover, and microtopographic structure, and (4) effects of fire on *Ribes* and other alternate hosts of white pine blister rust.

2. Materials and methods

2.1. Study area

We conducted our surveys at three high-elevation sites that were burned in high-severity wildfires of 1978 and contained one or both of our target species (Fig. 1). From north-to-south, these are the Ouzel Burn (Ouzel, Rocky Mountain National Park; 40.2°N, 105.6°W, 2720–3300 m; 436 ha), the Badger Mountain Burn (Badger, Pike-San Isabel National Forest; 39.1°N, 105.5°W, 3000–3300 m; 52 ha), and the Maes Creek Burn (Maes, Pike-San Isabel National Forest, 37.9°N, 105.0°W, 2960–3600 m; 946 ha). These burns were selected for sampling because (1) previous research (discussed above) indicated that regeneration of both species occurred primarily following stand-replacing fire, (2) an earlier study (A. Schoettle, unpublished data) suggested that more recent (post-1995) burns were unlikely to contain sufficient seedling densities to meet our research objectives, likewise, (3) older (late 19th C) burns contain primarily mature trees and conditions for seedling establishment are difficult to extrapolate, and (4) these burns were all large, easily located, and directly comparable because they occurred in the same year. Limber pine occurs at all three sites, but bristlecone pine does not extend as far north as Ouzel. All three sites are east of the continental divide in faulted, anticlinal mountain ranges formed during the Laramide Orogeny, and underlain by metasedimentary rocks originating 1.8 bya intruded by granite 1.4 bya.

The north-to-south arrangement of these sites is representative of the latitudinal gradient in precipitation seasonality and species composition that characterizes the southern Rocky Mountains (e.g., Peet, 1978). The general climate of the study area is semi-arid and continental, but precipitation peaks in the spring in mountains of northern Colorado (Ouzel) and in late summer farther south (Badger and Maes), where the influence of the North American Monsoon (Adams and Comrie, 1997) is stronger. Climate data from stations near our study sites—though at lower elevations—reflect this pattern (WRCC, 2008). Near Ouzel, Allenspark (40.2°N, 105.6°W, 2600 m) recorded an annual mean precipitation of 53.2 cm (1971–1993) with the wettest month being April (6.5 cm). The closest climate station to Badger Mountain, Lake George (38.6°N, 105.3°W, 2600 m), received a mean of 32.1 cm (1971–2000), with a precipitation peak in August (6.3 cm). East of Maes Creek, Rye (37.6°N, 104.6°W, 2600 m) recorded a mean of 56.7 cm (1971–2000), also with a maximum in August (8.6 cm).

Besides the addition of bristlecone pine at high elevations and the drop in the elevational range of limber pine in our two southern sites, changes in forest species composition from north-to-south include a decrease in lodgepole pine (*Pinus contorta*) and subalpine fir (*Abies lasiocarpa* var. *lasiocarpa*) near their southern geographic range limits; neither of these species were present at Badger or Maes. The ecological role of aspen (*Populus tremuloides*) becomes more important in the south where lodgepole pine is absent (Peet, 1978).

2.2. Field sampling

Sampling was conducted in plots positioned along 145-m transects crossing burn perimeters and stratified by elevation and aspect as follows. Prior to sampling, the perimeters of each burn were digitized into a GIS coverage, based on a combination of 2-m resolution aerial imagery, recent vegetation maps (Rocky Mountain N.P. and the Pike-San Isabel N.F.), and fire perimeter polygons (Pike-San Isabel N.F.). Each burn was divided into 100-m elevational bands and transects were placed across burn perimeters at random within each band, with at least one transect in each elevational band. Where burn perimeters within an elevation band covered a wide range of aspects—for example, where opposite sides of the burn had substantially different (>90°) orientations—we further subdivided elevational bands and added randomly placed transects within these divisions. Transects ran perpendicular to the burn perimeter, with five plots placed along each transect to capture a range of burn conditions. These included a plot at the partially burned edge (0 m), where intact forest abutted the burn, a sequence of plots at increasing distances (15, 45, and 100 m) into the interior of the burn—including mostly plots where canopy mortality had been complete, but infrequently including plots with only partial canopy mortality—and an unburned plot exterior to the burn and 45 m from the perimeter (−45 m). Between 28 June and 5 September, 2007, we sampled 190 plots on 38 transects: 70 plots at Ouzel, 40 at Badger, and 80 at Maes.

Sample plots were 5 m × 20 m, and oriented with the long axis perpendicular to the transect. At plot center, we collected the following data: spatial location (UTM NAD 83 Zone 13) and elevation using a handheld GPS unit with 15-m resolution (Garmin, Olathe, KS), percent slope (clinometer reading) and aspect (compass bearing). Plots were categorized into three classes of burn severity: complete burn (total canopy tree mortality), partial burn (evidence of fire, but some canopy trees persisting), and unburned (no evidence of recent wildfire). We measured basal area (at 1.4 m) and height of each tree (individual stems >2.5 cm dbh), and tallied saplings (stems >1.5 m tall, <2.5 cm dbh) and seedlings (stems 0.1–1.5 m tall) by tree species. Tree seedlings <0.1 m were not included in our tally. Stems occurring in clusters were each recorded separately. We visually estimated percent cover for each vascular plant species that occupied $>0.5\ \mathrm{m}^2$ (0.5% of the plot) using the following cover classes: 1%, 2–3%, 3–6%, 6–10%, 10–15%, 15–20%, and at increments of 10% up to 100%. We also visually estimated percent ground cover by cryptograms, woody debris, leaf litter, bedrock (>4096 mm), boulders (>256–4096 mm), cobbles (>64–256 mm), gravel (>2–64 mm), and mineral soil (<2 mm).

Seedling microsite conditions were sampled in nested, 0.25 m × 0.25 m subplots. Four microsite subplots were placed randomly within the plot, one in each 5 m × 5 m quarter. We also centered 0.25 m × 0.25 m microsite subplots on each bristlecone and limber pine seedling in the plot. In each of these microsite subplots, we estimated percent cover by tree seedlings, shrubs, forbs, and graminoids, and listed the most abundant species in each layer. We also estimated percent ground cover using the same categories as in the larger plots (listed above), and measured the maximum litter and duff depth to mineral soil or rock. From the center of each microsite subplot, we measured the distance to the nearest three structural objects. Objects were defined as measuring >10 cm in two perpendicular dimensions, and categorized as boulders, cobbles, fallen woody debris, or standing tree trunks. We took a digital hemispheric photo of the canopy at a height of 1 m above each random microsite subplot, and from the top of each sampled seedling, during uniformly cloudy or twilight conditions.

2.3. Statistical analysis

Because our size class data exhibited a clear gap between stems <10 cm dbh (post-1978 regeneration) and stems >10 cm (older trees in intact stands or burn-survivors), for several analyses we grouped all stems <10 cm, collectively referred to as post-fire tree regeneration. We tested for relationships between post-fire regeneration density, burn severity, and distance to seed source, and regeneration density and all other plot-level factors (e.g., elevation, bedrock cover), including coverages by plant life forms (trees, shrubs, forbs, and graminoids). Aspect was transformed to a SW-to-NE index [−cosine(aspect − 45°)]. We tested for relationships between seedling presence/absence at the subplot scale and all factors measured at the plot- and subplot-level (including life-form cover but not cover by individual species, at both scales). We tested for associations between individual plant species and presence of bristlecone or limber pine seedlings at the subplot scale, across all sites. Hemispheric photos were analyzed using the software Hemiview 2.1 (Delta-T Devices, 1999) to calculate canopy cover, sky cover, and total direct and indirect radiation above each subplot.

To test for relationships between post-fire regeneration density (at the level of the 100-m^2 plot), seedling presence (at the 0.25-m^2 subplot level), and predictor variables, we used generalized linear mixed-effects models (glmm's) as implemented using the *glmmPQL* function in the R software package. In classical statistics, all observations are assumed to be independent, which may lead to misleading inferences when observations are in fact clustered in space or time (as they are in most ecological datasets) and subject to unmeasured but autocorrelated processes. Mixed-effects models address clustering by assuming two sources of variation: variation within clusters and variation between clusters. We took advantage of the capacity of glmm's to (1) model non-normally distributed response variables (in our case, a binomial distribution of microsite presence/absence and a Poisson distribution of counts of stems in plots), and (2) account for the clustering of observations (within plots, transects, and study sites) by modeling each level of nesting as a random effect. We analyzed bristlecone pine and limber pine separately, and tested for their responses to measured environmental factors across all sites and at each site individually. Model selection consisted of three steps. First, we screened each predictor variable using the appropriate glmm; only predictor variables significant at $P < 0.25$ were included in subsequent multiple regression models, following the procedure recommended by Hosmer and Lemeshow (2000). Secondly, we used backwards elimination to identify the generalized linear model (excluding random effects), that minimized Akaike's Information Criterion (AIC). We then added the random effects to this model, and eliminated any terms that were not significant at $P < 0.05$.

We also used (logistic) generalized linear mixed-effects models to test for differences between unburned, partially burned, and completely burned plots on the frequency of *Ribes*, *Castilleja*, and *Pedicularis*. We used chi-square tests to examine associations between *Ribes* spp., *Castilleja* spp., *Pedicularis* spp., and limber or bristlecone pine regeneration at the plot level. We tested for associations between all *Ribes* and both five-needle pines collectively, and also each *Ribes*–*Pinus* species pair separately. Because we had many fewer samples that contained *Castilleja* or *Pedicularis*, we tested for associations between each of these genera and both five-needle pines, but did not test each species pair separately. We also used chi-square tests and comparisons of multiple proportions (Goodman, 1964) to check for different proportions of clustered seedlings between species, between sites, and between and burn severity class (e.g., are clustered seedlings more frequently encountered in burns?).

3. Results

3.1. Density and pattern of post-fire regeneration

The abundance of post-wildfire regeneration (the sum total of seedlings, saplings, and small trees <10 cm dbh) exhibited considerable variation between five-needle pine species and sites (Tables 1 and 2; Fig. 2). Regeneration density in sampled plots ranged from 0 to 1800 ha^{-1} for bristlecone pine and from 0 to 3000 ha^{-1} for limber pine. Mean bristlecone pine regeneration density was 310 ± 46 ha^{-1} (mean ± 1 S.E.) at Badger and 65 ± 29 ha^{-1} at Maes. We observed high levels of bristlecone pine regeneration at the burn edge at Maes and at 15 m into the burn at Badger (Table 1; Fig. 2). Limber pine regeneration at Ouzel averaged 314 ± 72 ha^{-1}; at Badger, 38 ± 30 ha^{-1}; at Maes, 68 ± 19 ha^{-1}. The spatial pattern of limber pine regeneration within each burn varied among sites (Fig. 2a–c): greatest in the burn interior at Ouzel and Badger, but concentrated in unburned plots at Maes, with another peak at the farthest sampled distance into the burns (100 m). Across all sites, five-needle pine regeneration was dwarfed by that of other species—often by one or two orders of magnitude (Table 1). Engelmann spruce (*Picea engelmannii*) and aspen (*P. tremuloides*) were especially abundant in burn edges and interiors.

Generalized linear mixed-effects model results suggest that these divergent patterns are imparted both by preferential establishment in different burn classes as well as variation in propagule dispersal distances, as measured by proximity to seed trees (Table 2). When modeled across both study areas (with study area included as a random factor), bristlecone pine showed nearly

Table 1
Densities (stems ha^{-1} ± 1 S.E.) of recent regeneration (stems <10 cm dbh) and older trees (>10 cm dbh) for the most abundant species, and both five-needle pines, by burn severity category, in each of the three study areas.

Species	Maes			Badger			Ouzel		
	Unburned	Partial burn	Complete burn	Unburned	Partial burn	Complete burn	Unburned	Partial burn	Complete burn
Regeneration stems <10 cm dbh ha^{-1}									
Abies lasiocarpa	0	0	0	0	0	0	5486 ± 846	4207 ± 949	2298 ± 630
Picea engelmannii	675 ± 258	689 ± 304	454 ± 222	67 ± 37	900 ± 313	1694 ± 1024	979 ± 230	1107 ± 265	2158 ± 453
Pinus contorta	0	0	0	0	0	0	21 ± 15	480 ± 270	1268 ± 342
Populus tremuloides	900 ± 336	2211 ± 797	4639 ± 834	367 ± 190	2377 ± 482	5739 ± 1037	36 ± 36	427 ± 358	2019 ± 504
Pinus aristata	38 ± 20	173 ± 99	33 ± 12	167 ± 44	453 ± 100	278 ± 90	0	0	0
Pinus flexilis	125 ± 62	56 ± 25	52 ± 23	0	54 ± 24	44 ± 22	43 ± 29	113 ± 45	480 ± 114
Residual trees stems >10 cm dbh ha^{-1}									
Abies lasiocarpa	0	0	0	0	0	0	457 ± 136	200 ± 56	10 ± 6
Picea engelmannii	325 ± 133	189 ± 72	0	244 ± 150	38 ± 31	0	214 ± 55	167 ± 44	5 ± 3
Pinus contorta	0	0	0	0	0	0	121 ± 46	93 ± 52	37 ± 13
Populus tremuloides	287 ± 124	72 ± 50	35 ± 23	33 ± 24	69 ± 40	161 ± 88	0	0	0
Pinus aristata	100 ± 59	72 ± 25	4 ± 3	322 ± 62	284 ± 46	0	0	0	0
Pinus flexilis	81 ± 36	83 ± 32	0	11 ± 11	54 ± 29	0	185 ± 90	80 ± 49	0

Table 2
Generalized linear mixed-effects model parameters (partial Poisson regression coefficients) for factors predicting the density of recent regeneration (stems <10 cm dbh) of bristlecone and limber pine relative to that in unburned stands, across all sites and for each site separately.

Parameter	Bristlecone pine			Limber pine			
	All sites	Maes	Badger	All sites	Maes	Badger	Ouzel
Seed-source distance	**−0.37*****	**−0.51*****	−0.36	**−0.20***	−0.10	**−0.41***	**−0.36***
Partial burn	**1.13*****	**1.61****	**0.94***	0.13	**−0.92***	1.60	0.96
Complete burn	**1.22*****	0.72	1.53	**1.61*****	−0.64	2.00	**3.41*****

Parameters that were significant at $P < 0.05$ are in bold, P-values are represented as follows.

[*] $P < 0.05$.

[**] $P < 0.01$.

[***] $P < 0.001$.

equivalent increases in regeneration in both burn categories relative to unburned locations; however, for models from each individual site, regeneration was significantly boosted only in partially burned stands (Table 2). When data from all three study areas were included in the same model, limber pine regeneration showed significant increases relative to unburned sites only where post-fire canopy mortality was complete. However, this pattern was inconsistent between models for individual study areas. At Ouzel, regeneration increased only in the completely burned stands, but limber pine exhibited no significant increases in regeneration in either burn category at Badger, and a significant decrease in partially burned stands at Maes. For both species, and across most study areas, regeneration density was negatively related to distance from the nearest potential seed source. For models incorporating data from all sites, bristlecone pine was more strongly depressed by seed-source distance than limber pine regeneration (glmm coefficients for log-distance (m) to seed source of −0.37 vs. −0.20; Table 2).

Did fire increase the absolute populations (all size classes) of either species on the landscape? Total bristlecone pine numbers were boosted only at burn edges and not in the burn interior at Maes (glmm P-value = 0.002; d.f. = 62; Table 1; Fig. 3); Badger exhibited a similar but non-significant pattern (glmm P-value = 0.12; d.f. = 30; Fig. 3). However, even in many stands

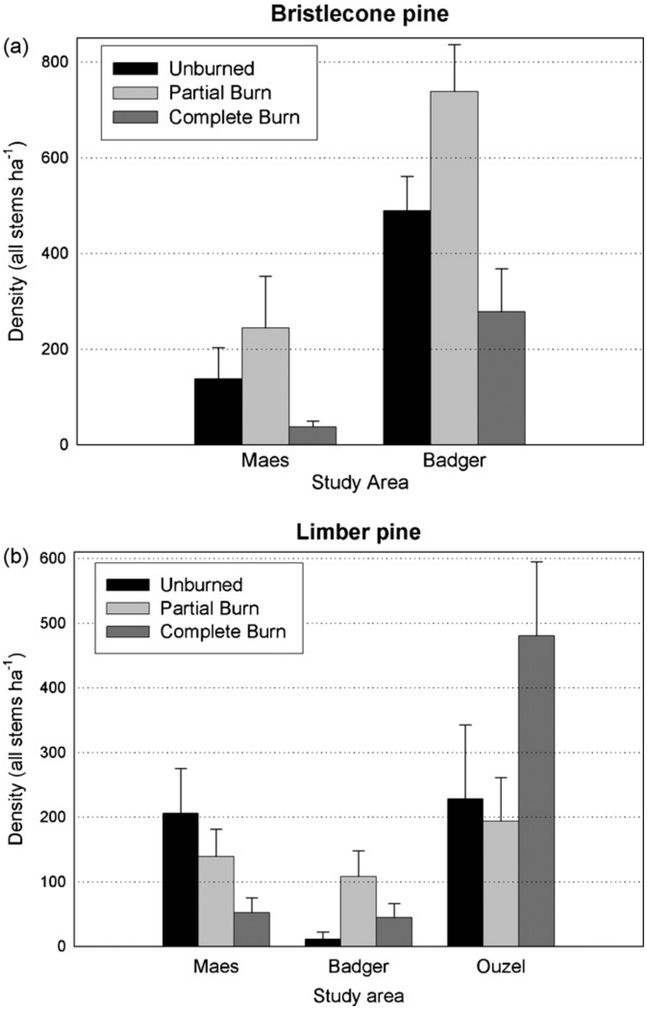

Fig. 3. Total densities (all size classes, stems ha^{-1}) of bristlecone pine (a) and limber pine (b), in the each burn class: unburned, partial burn (incomplete canopy mortality from 1978 fire), and complete burn (complete canopy mortality caused directly or indirectly by 1978 fire). Error bars represent 1 S.E.

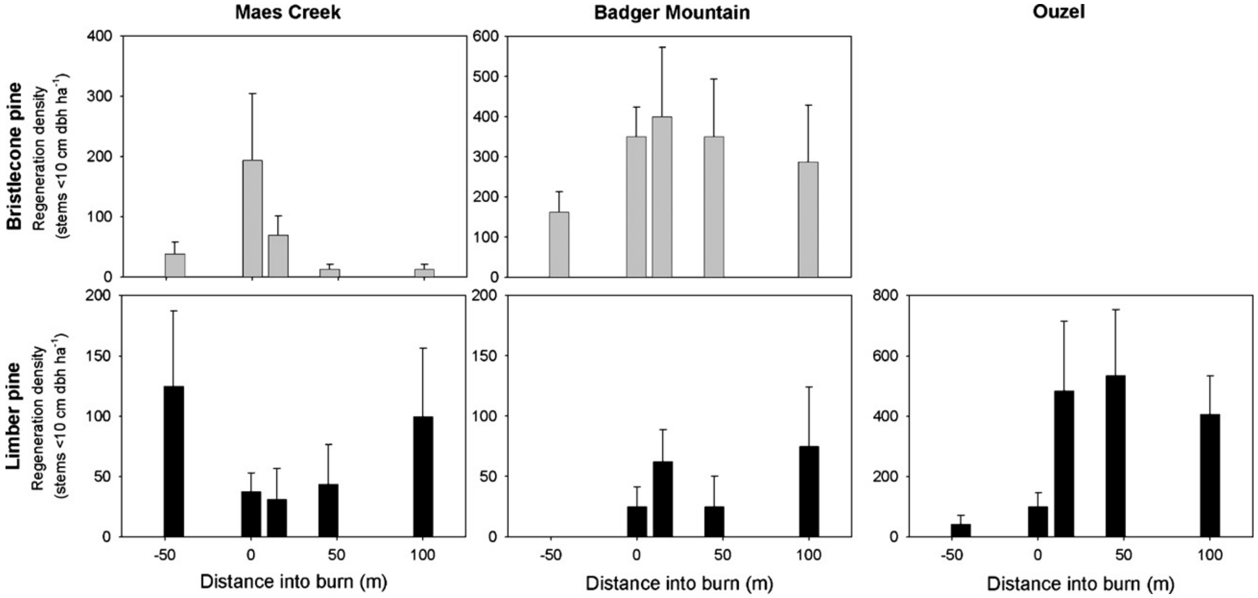

Fig. 2. Density (stems ha^{-1}) of recent bristlecone and limber pine regeneration (all stems <10 cm dbh) and distance (m) from the burn margin (0 represents burn edge) across all three study sites, Maes Creek, Badger Mountain, and Ouzel. Error bars represent 1 S.E.

Table 3
Number of bristlecone and limber pine seedlings sampled, proportion of seedlings occurring in multi-stem clusters at all sites together and each site separately, distances from clustered and unclustered seedlings to the nearest seed source (±1 S.E.), and mean cluster size (±1 S.E.).

	Bristlecone pine			Limber pine			
	All sites	Maes	Badger	All sites	Maes	Badger	Ouzel
Seedlings sampled (n)	132	47	85	242	48	16	178
Proportion occurring in stem clusters	0.12	0.13	0.12	0.54	0.46	0.25	0.59
Clustered seedlings mean distance to seed source (m)	6.5 ± 3.8	2.3 ± 1.5	9.0 ± 6.0	85.5 ± 11.9	147.6 ± 66.8	17.5 ± 4.3	76.5 ± 6.3
Unclustered seedlings mean distance to seed source (m)	7.0 ± 1.4	5.0 ± 2.6	8.1 ± 1.3	41.4 ± 7.3	21.8 ± 5.5	20.8 ± 5.3	51.8 ± 10.7
Mean size (number of seedlings) of all stem clusters	2.3 ± 0.3	2.0 ± 0.0	2.5 ± 0.5	2.8 ± 0.3	2.2 ± 0.1	2.0 ± 0.0	3.1 ± 0.3

where abundance was boosted by fire, relative abundance was actually lower due to far greater proportional post-fire increases by other tree species (Table 1). For limber pine, absolute abundance rose in the burn interior at Ouzel (glmm P-value = 0.045; d.f. = 54; Table 1; Fig. 3) At Badger, limber pine showed increases only in such partially burned sites Finally, at Maes, limber pine populations showed reductions in high-severity burns (glmm P-value = 0.002; d.f. = 62; Table 1, Fig. 3).

3.2. Stem clusters

Limber pine seedlings more frequently occurred in clusters (54% of all seedlings were clustered) than bristlecone pine (12%; Table 3, $P < 0.001$ for χ^2-test, d.f. = 1). Sites differed in the number of clustered limber pine seedlings ($P = 0.015$ for χ^2-test with 2 d.f.): Ouzel contained more clustered limber pine seedlings than Badger ($P < 0.05$, multiple proportions test; Table 3), but neither differed significantly from Maes. Clustered limber pine seedlings exhibited different relationships to burn severity ($P < 0.0001$ for χ^2-test, d.f. = 2) than non-clustered seedlings; plots with complete canopy mortality showed greater frequencies of clustered limber pine seedlings than those where canopy mortality was partial ($P < 0.05$, multiple proportions test). Clustered limber pine seedlings were also encountered at greater distances from seed-source trees than solitary seedlings [85.5 ± 11.9 m vs. 41.4 ± 7.3 m (mean ± 1 S.E.); $P < 0.0001$ for 2-tailed t-test of log-transformed distances, d.f. = 240]. On the other hand, clustered bristlecone pine seedlings were found in the same proportions in each burn category and at the same distance from seed-source trees as non-clustered seedlings. Limber pine seedlings occurred at greater distances from a seed source than bristlecone pine, regardless of clustering (65.3 ± 7.4 m vs. 6.9 ± 1.2 m; $P < 0.0001$, d.f. = 268). For both species, clustered seedlings did not show different proximity to surface objects, nor different affinities to types of objects (discussed in more detail below), as non-clustered seedlings.

3.3. Seedling microsites, objects, and plant associates

Environmental factors that significantly predicted seedling presence in sampled 0.25 m^2 subplots within our larger 100 m^2 plots, as identified by generalized linear mixed-effects models, are listed in Table 4. At the subplot level, both microtopographic structure (object distances), ground cover (cover by cobbles, mineral soil, standing tree trunks, and leaf litter), and canopy cover (total sky cover) all were significantly associated with seedling establishment in at least one model. The role of objects is given more consideration below. Cover by cobbles was a positive predictor of seedling presence for bristlecone pine at Badger, but was negative for limber pine in three of four models. Mineral soil cover was also a negative predictor of seedling presence in several models. Leaf litter and tree trunks (estimated percent cover of subplots occupied by the bases of trees) were positive predictors of limber pine seedling presence in several models. Cover by gravel, mosses, graminoids, forbs, shrubs, and other tree seedlings were not retained as significant predictors of seedling presence in these models. Limber pines seedlings were also found in subplots with higher values of open sky cover at Ouzel and Badger, as were

Table 4
Generalized linear mixed-effects model parameters (partial logistic regression coefficients) predicting the presence of seedlings in 0.25-m^2 subplots.

Parameter	Bristlecone pine			Limber pine			
	All sites	Maes	Badger	All sites	Maes	Badger	Ouzel
Subplot-level factors (0.25 m^2)							
Nearest 3 objects mean distance	-0.01^{***}		-0.02^{*}	-0.02^{***}	-0.02^{**}		-0.03^{**}
Nearest object distance						-0.07^{***}	
Mineral soil	-0.05^{**}		-0.04^{*}	-0.04^{**}			
Cobbles			0.06^{*}	-0.04^{***}	-0.10^{***}	-0.48^{*}	
Tree trunk				0.05^{**}	0.16^{***}	0.46^{***}	
Leaf litter				0.02^{***}		0.10^{***}	0.02^{***}
Sky			3.27^{*}	2.60^{***}		6.22^{*}	2.36^{*}
Plot-level factors (100 m^2)							
Seed-source distance	-0.65^{***}	-0.68^{***}	-0.35^{*}				
Aspect	0.63^{*}						0.79^{*}
Elevation					-0.01^{***}		
Cobbles					0.09^{**}		
Leaf litter				-0.04^{***}			-0.05^{***}
Forb cover			0.08^{***}			0.34^{***}	
Graminoid cover						-0.30^{***}	0.06^{*}
Understory cover		-0.03^{**}					

Factors not significant at $P < 0.05$ were not included in any model. P-values are represented as follows.
[*] $P < 0.05$.
[**] $P < 0.01$.
[***] $P < 0.001$.

bristlecone pine seedlings at Badger. Measures of estimated direct radiation above seedlings were not retained as significant in any model.

At the plot level, distance to seed source was negatively related to bristlecone pine, but not limber pine establishment (Table 4). Topographic factors (aspect and elevation, but not slope) and ground cover (leaf litter, cobbles, forbs, graminoids, and total understory cover) were also associated with seedling establishment. Models for bristlecone pine across sites, and for limber pine establishment at Ouzel, indicated that establishment was higher on SW-facing slopes. Limber pine establishment occurred at lower elevation of the Maes Creek burn. Where significant, leaf litter was negatively related to establishment probability at the plot level, forb cover was positive, and graminoid cover exhibited both positive and negative relationships. Total understory cover was negatively related to bristlecone pine seedling establishment at Maes.

Seedlings of both species exhibited very strong spatial affinities to objects across nearly all sites (Table 4); categories of surface objects >10 cm × 10 cm included standing tree trunks, woody debris, cobbles and boulders. The mean distance from the closest three objects was a strong negative predictor of bristlecone pine seedling presence at Badger and for models incorporating data from both sites (Table 4); limber pine presence was better predicted by the distance to the single closest object only at Badger. Seedling affinity to objects extended to at least the nearest three objects that we sampled (Fig. 4). Bristlecone pine seedlings were found at 16.6 ± 28.1 cm from the nearest single object (vs. 26.2 ± 35.5 cm for random subplot centers) and at a mean distance of 31.9 ± 40.8 cm from each of the nearest three objects (vs. 47.6 ± 53.9 cm). Limber pine seedlings occurred at 11.0 ± 12.9 cm (vs. 23.3 ± 32.7 cm for random subplot centers) from the nearest object and at an average distance of 23.6 ± 16.6 cm (vs. 43.2 ± 46.2 cm) from nearest three objects. Seedlings were not associated with any particular category of object (e.g., cobbles, tree trunks, etc.) at greater or lower frequencies than expected based on the occurrence of that object type across the landscape (glmm $P > 0.05$, d.f. = 491 for bristlecone pine; glmm $P > 0.05$, d.f. = 811 for limber pine).

Limber pine seedlings were positively associated with fireweed (*Chamerion angustifolium* (L.) Holub; glmm $P < 0.0001$, d.f. = 810) and kinnikinnick (*Arctostaphylos uva-ursi* (L.) Spreng.; $P < 0.0001$, d.f. = 810) in subplots. Bristlecone pine seedlings were associated with purple reedgrass (*Calamagrostis purpurascens* R.Br.; glmm $P = 0.030$, d.f. = 489), Parry's goldenrod (*Oreochrysum parryi* (A. Gray) Rydb., $P = 0.015$, d.f. = 489), and common juniper (*Juniperus communis* L.; $P = 0.045$, d.f. = 489).

3.4. Effects of fire on Castillja, Pedicularis, and Ribes

We encountered three species of *Castilleja*, wholeleaf Indian paintbrush (*C. integra* Gray), giant red Indian paintbrush (*C. miniata* Dougl.), and western Indian paintbrush (*C. occidentalis* Torr.), and three species of *Pedicularis*, elephanthead (*P. groenlandica* Retz.), Parry's lousewort (*P. parryi* Gray), and sickletop lousewort (*P. racemosa* Dougl.) in our samples. At least one species of *Castilleja* was found on 27/200 plots, and one species of *Pedicularis* occurred on 8/200 plots. We encountered four species of *Ribes* across all sampled plots, wax current (*R. cereum* Douglas), whitestem gooseberry (*R. inerme* Rydb.), trailing black current (*R. laxiflorum* Pursh), and gooseberry current (*R. montigenum* McClatchie). At least one species of *Ribes* was found on 50 of 200 sample plots. Relative to unburned stands, *Castilleja* occurrence increased in both partial burns (glmm $P < 0.05$, d.f. = 158; Fig. 5) and completely burned stands (glmm $P < 0.001$, d.f. = 158, Fig. 5), *Pedicularis* decreased in complete burns (glmm $P < 0.001$, d.f. = 158, Fig. 5), and *Ribes* was elevated in both burn categories ($P < 0.05$ for partial burns, and $P < 0.001$ for complete burns, d.f. = 158; Fig. 5). However, seedlings and saplings of five-needle pines and alternate hosts of white pine blister rust were not consistently found together in our 100-m^2 plots. *Castilleja* was not associated with five-needle pine regeneration at the 100-m^2 plot level ($P = 0.9$, χ^2-test, d.f. = 1). We had too few observations of *Pedicularis*

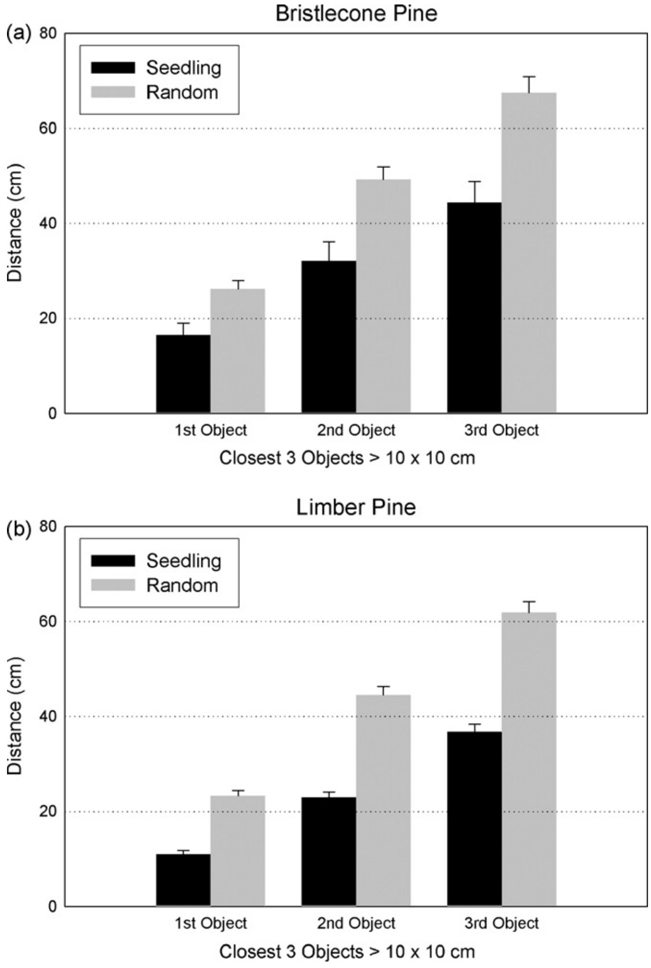

Fig. 4. Measured distances from bristlecone (a) and limber pine (b) seedlings and random points to the closest three objects >10 cm × 10 cm, including cobbles, boulders, down logs, and bases of standing trees. Error bars represent 1 S.E.

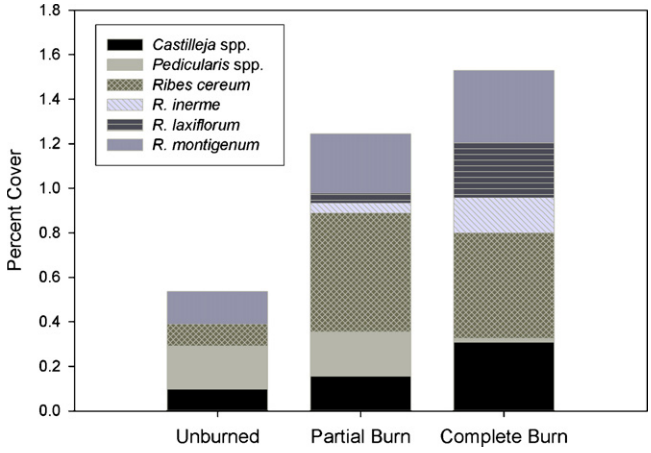

Fig. 5. Cover by alternate host species of white pine blister rust in each fire severity classes, averaged across all plots at all three sites.

(8 occurrences) for statistical tests of association, but all of these occurred in plots where five-needle pines were absent. Collectively, *Ribes* spp. showed a slight positively association with bristlecone and limber pine regeneration ($P = 0.04$, χ^2-test, d.f. = 1). Because *Ribes* species vary in their susceptibility to white pine blister rust (summarized in Van Arsdel and Geils, 2004)—and thus their capacity to serve as alternate hosts for the pathogen—we also considered each species of *Ribes* and each five-needle pine species separately. We found that wax current was positively associated with bristlecone pine regeneration ($P < 0.001$). However, no other species of *Ribes* was associated with bristlecone pine regeneration, and no species was associated with limber pine ($P > 0.05$).

4. Discussion

4.1. Differences between bristlecone and limber pine

Taken as a whole, fire increased both bristlecone and limber pine seedling establishment (Fig. 3), but with important distinctions between species, between burn severity classes (partial vs. complete canopy mortality), and between the three burns we sampled (Table 1; Fig. 2). However, across sites, both species exhibited a very prolonged regeneration dynamic, and nearly thirty years after fire, total tree densities of both species in burns had not yet reached the densities in nearby unburned stands (Table 1; Fig. 3). Densities of post-fire regeneration by competing tree species, particularly aspen and Engelmann spruce, were frequently one to two orders of magnitude greater than that of either five-needle pine species (Table 1). As a consequence, even where numbers of five-needle pines were raised in burns, relative abundance was often lowered.

The post-fire regeneration dynamic of limber pine at Ouzel—with substantial establishment in the burn interior distant from seed sources (Fig. 2; Tables 2 and 3), and a net increase in population size in plots with complete canopy mortality (Fig. 3)—is consistent with the findings of previous research on limber pine stand dynamics in subalpine forests of the northern Front Range of Colorado (Veblen, 1986; Rebertus et al., 1991). Limber pine appears to exhibit a metapopulation dynamic in these systems, colonizing the interior of spatially extensive, high-severity burns, then gradually facilitating its own replacement by more shade-tolerant spruce and fir (Donnegan and Rebertus, 1999). The pace of limber pine colonization and eventual replacement is delayed by increasing elevation and on more xeric aspects (Shankman and Daly, 1988; Donnegan and Rebertus, 1999). Fire appeared to promote limber pine regeneration at Ouzel through both the removal of canopy shade and alteration of the ground layer (including decreased leaf litter but greater graminoid cover at the 100-m^2 plot scale; Table 4). As with seral subalpine stands of whitebark pine farther north in the Rockies (Arno, 2001) these populations may require infrequent, stand-replacing fires to create habitat for seedling establishment. In the absence of disturbance, successional processes may wedge the species out of mesic subalpine landscapes through shading and litter accumulation that favors more shade-tolerant species such as Engelmann spruce and subalpine fir, which can become established in deep needle litter.

Farther south, bristlecone pine showed some similarities in its pattern of post-fire regeneration where it was dominant in the dry subalpine forests at Badger Mountain and Maes Creek, but also some important differences that appear related to differences in seed dispersal. Bristlecone pine seedling establishment was increased in burns (Table 2), findings which are largely consistent with those of Baker (1992), who concluded that high-severity fire promoted bristlecone pine regeneration. However, in contrast to limber pine regeneration at Ouzel, bristlecone pine regeneration tended to be concentrated near or beneath surviving trees at the burn edges (Fig. 2; Tables 2 and 3). Overall, populations showed decreases in burn interiors generated by the high-severity fires of 1978 (Fig. 3). This pattern appears to be largely driven by poor seed dispersal into burn interiors, as reflected by strong decreases in seedling abundance with distance from seed sources (Tables 2–4).

Limber pine also appeared to exhibit a shift in its regeneration ecology from Ouzel—where seedlings preferentially established in the high-severity burn interior—to Badger and Maes—where regeneration in burn interiors was poor (Fig. 2; Table 2). Explanations for this change in regeneration pattern could include altered dispersal processes that resulted in fewer propagules reaching the burn interior, or differential growth or survival in burn interiors due to environmental conditions at the southern sites. We found little evidence, in the form of seed-source distance and seedling clusters (Table 3, discussed more below), for reduced nutcracker seed dispersal at Badger and Maes. However, the change in regeneration pattern from north-to-south was accompanied by a decrease in limber pine seedling height growth (J. Coop, unpublished data), suggesting declining seedling physiological performance under the environmental conditions present at the southern sites relative those in the north, possibly related to differences in precipitation quantity and seasonality, or the frequency of severe drought.

The different patterns of regeneration between species and study areas appear attributable to both the influences of post-fire environmental conditions on seedling establishment as well as different seed dispersal mechanisms, as evidenced by characteristic seedling distances from seed sources and frequencies of seedling clusters (Tables 3 and 4). Limber pine seedlings exhibited much greater clustering than bristlecone pine seedlings across sites, consistent with expected differences between bird- and wind-dispersal. The 25–59% of limber pine seedlings we recorded in clusters (Table 3) is well within the range of clustering of limber pine elsewhere in Colorado (Carsey and Tomback, 1994; Schoettle and Rochelle, 2000), and that reported for several other species of Clark's nutcracker-dispersed pines (Lanner, 1996). Though both solitary and clustered limber pine seedlings may have originated from bird-dispersed seeds, we found divergent spatial patterns: clusters occurred at greater distances from potential seed trees and more frequently in severely burned plots. These findings suggest limber pine seed dispersal by Clark's nutcrackers into more distant and open areas. Not only was clustering far less common for bristlecone pine seedlings, but it was not associated with increased dispersal distance or greater establishment in burn interiors (Table 3). The 12% clustering we observed in bristlecone pine may suggest a minor role of animal-caching, but given the comparable dispersal distances and environments of clustered and solitary bristlecone pine seedlings, it appears unlikely that these clusters are arising from nutcracker caches. Instead, seeds may have been transported short distances by seed-caching rodents, secondary to wind-dispersal (e.g., Vander Wall, 1992; Tomback et al., 2005).

4.2. Topographic structure and seedling microenvironment

Facilitation may be an essential process in tree seedling establishment at high-elevation sites, especially near alpine treeline in the Rockies (Smith et al., 2003). We uncovered strong evidence for the promotion of bristlecone and limber pine seedling establishment by "nurse objects" including cobbles, boulders, fallen logs, and standing tree trunks (Table 4; Fig. 4), but only ambiguous evidence for any facilitation of seedling establishment by neighboring plants. Across sites, seedlings of both species showed strong association to objects > 10 cm $\times$ 10 cm (Table 4). Clark's nutcrackers are known to cache seeds near rocks, woody debris, tree trunks, and living vegetation (Tomback, 1982); however, the association with objects we found is not solely related to nutcracker dispersal, as it was also prevalent in wind-dispersed bristlecone pine. Instead, objects may enhance conditions for seedling establishment by ameliorating the local abiotic or biotic environment. At alpine treelines, structures offering topographic shelter have been shown to increase both tree seedling establishment and survival (Resler et al., 2005). Objects may afford direct protection from wind, ice-blasting, solifluction, snow creep, or other physical disturbances. Small snowdrifts captured in the lee of the objects we recorded may also provide winter protection from ice-blasting, excessive solar radiation, and thermal extremes, as with snow captured within krummholz mats (Hadley and Smith, 1987), as well as increase soil moisture availability in the spring. Water running off of the impermeable surfaces of objects may also increase nearby soil moisture availability throughout the year. Finally, objects may also hide seeds from seed-predators (Munguía-Rosas and Sosa, 2008). The relationship between seedlings and nurse objects that we found appears to extend beyond the single closest object, to at least as far as the three nearest such objects (Fig. 4), implying additional protective effects of multiple objects, or perhaps a benefit of general microtopographic roughness. Distance to the mean of the three closest objects was generally a stronger (negative) predictor of seedling presence than distance to the single closest object (Table 4). Interestingly, we did not detect any seedling "preference" towards one type of object over another (i.e., cobbles vs. tree trunks), suggesting different types of objects afforded similar benefits to seedling establishment.

We found no positive relationship between plant cover, or cover by different life forms (cryptograms, graminoids, forbs, shrubs, or trees) on seeding presence at the microsite-scale, though we did find both positive and negative relationships at the plot-scale (Table 4). We found significant positive associations between seedlings and several other plant species: bristlecone pine with purple reedgrass, Parry's goldenrod, and common juniper; limber pine with fireweed and kinnikinnick. It is more likely that these associations represent shared affinities toward a similar set of environmental conditions by multiple species rather than interspecific facilitation of uncertain mechanism, given the physiognomic and taxonomic diversity within these sets of species. The negative relationship we found at some sites between seedling presence and both exposed mineral soil and cobble cover may be indicative of recent disturbance or continuing post-fire erosion prohibitive of any plant establishment. Likewise, leaf litter cover (positively related to seedling presence at the microsite-scale) is probably an indicator of sites that are stable enough to maintain post-fire plant growth and litter deposition. However, leaf litter cover at the plot-scale—mostly needle litter associated with dense conifer cover—was negatively associated with limber pine establishment in two models. Limber pine at Badger and Ouzel, and bristlecone pine at Badger also clearly benefitted from the removal of forest canopy, as shown by positive effects of sky cover (Table 4).

4.3. Management implications

Our findings bear directly on current and proposed management of both bristlecone and limber pine stands in Colorado. Both species are highly vulnerable to white pine blister rust, and proactive management has been proposed to mitigate population declines, genetic losses, compositional turnover, and changes to ecosystem processes that blister rust is likely to cause (Schoettle and Sniezko, 2007). Potentially useful strategies include outplantings of rust-resistant seedlings and silvicultural treatments that maintain or boost populations and diversify age-class structure (primarily via increases in younger cohorts) prior to rust outbreaks (Schoettle and Sniezko, 2007).

The prolonged population response to natural disturbance that we observed suggests that responses to stand management are likely to be slow. In particular, treatments intended to promote or augment regeneration may require many decades before positive effects are realized. Given the expansion of white pine blister rust into the southern Rockies and time frame over which we may expect to see rust-driven stand decline, development and application of such treatments may yield greater benefits where they are conducted sooner, rather than later. In southeastern Wyoming, Kearns and Jacobi (2007) estimated that an average disease incidence of 15.5% of limber pine had been reached in only 2–4 decades, with >50% of stands infected. Blister rust has led to massive mortality among high-elevation whitebark pine in the Idaho, Montana, and northwestern Wyoming in the ca. 70 years since it was first recorded in that region (McDonald and Hoff, 2001). Combined with expected blister rust spread is the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemic that is resulting in mortality of mature bristlecone and limber pines in parts of Colorado (USDA Forest Service, Region 2 Forest Health Management). As mature trees die in these areas, management options may become limited by inadequate seed sources. The rapid implementation of alternative approaches—including protection of populations known to contain rust-resistant individuals from beetles (e.g., spraying), rust resistance screening, seed collection, and outplanting—appear critical to mitigate long-term stand declines (Schoettle et al., 2008).

For fire or silvicultural treatments to effectively boost bristlecone and limber pine populations, we offer the following suggestions based on our findings. Greater dependence on nearby seed source for bristlecone pine and the greater numbers of seedlings in plots that retained living canopy trees suggest that mixed-severity burns that create small openings (≤15 m) should be most effective at promoting regeneration. Limber pine populations in the northern part of the southern Rockies appear to benefit from high-severity, spatially extensive fires, but this may not be the case farther south. However, we note that these findings are drawn from a small sample of burns (3), and to assess their generality would require more research from a larger number of burns throughout the range of bristlecone and limber pine. The much greater proportional increases by other tree species following fire in many sites also suggests that single treatments may be ineffective, and subsequent steps may be required to reduce the effects of competition on five-needle pine growth and/or survival.

Seedling establishment of both bristlecone and limber pine is enhanced by microtopographic structure including boulders, cobbles, logs, and tree trunks (alive or dead), and management geared towards promoting regeneration should ensure high densities of such objects. Future outplantings of rust-resistant seedlings could also take advantage of objects. As has been proposed for whitebark pine outplanting (Scott and McCaughey, 2006), seedlings of both bristlecone and limber pine are likely to benefit when planted adjacent to objects, especially in areas affording shelter by several objects. Regardless of recent fire history or stand management, good microsites for bristlecone pine seedlings may be further indicated by purple reedgrass, Parry's goldenrod, and common juniper; microsites for limber pine outplantings may be indicated by fireweed and kinnickinnick.

Finally, openings (produced by fire or silviculture) appear likely to increase cover and frequency of *Ribes* and *Castilleja* species (Fig. 5), alternate hosts of white pine blister rust. Whether or not such changes could influence future white pine blister rust outbreaks in these stands is uncertain. Collectively, cover by alternate hosts together was greater in burns than in adjacent unburned stands, though still averaging <2%. Only one of these alternate host species [*R. cereum*, considered a poor host for white pine blister rust (Van Arsdel and Geils, 2004)] was positively associated with regeneration by either five-needle pine at the 100-m^2 scale. However, local host densities and spatial associations between hosts and five-needle pines may have little influence on white pine blister rust hazard in upland habitats of the Western U.S. Newcomb (2003) suggests that landscape context (e.g., distance to riparian patches of more susceptible hosts such as *R. hudsonianum* and *R. lacustre*) is a far more important determinant of blister rust disease hazard than the local host associations. While altered disease hazard from altered host cover in burns (or silvicultural treatments) thus remains an uncertainty, it may not necessarily offset benefits—including population maintenance during natural selection for rust resistance—of increased regeneration by five-needle pines.

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