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Subalpine vegetation pattern three decades after stand-replacing fire: effects of landscape context and topography on plant community composition, tree regeneration, and diversity

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Abstract

Objective: Our purpose was to characterize vegetation compositional patterns, tree regeneration, and plant diversity, and their relationships to landscape context, topography, and light availability across the margins of four stand-replacing subalpine burns.

Location: Four 1977 to 1978 burns east of the Continental Divide in Colorado: the Ouzel burn, a burn near Kenosha Pass, the Badger Mountain burn, and the Maes Creek burn.

Methods: Vegetation and environmental factors were sampled in 200 0.01-ha plots on transects crossing burn edges, and stratified by elevation. We utilized dissimilarity indices, mixed-effects models, and randomization tests to assess relationships between vegetation and environment.

Results: Three decades after wildfire, plant communities exhibited pronounced compositional shifts across burn edges. Tree regeneration decreased with increasing elevation and distance into burn interiors; concomitant increases in forbs and graminoids were linked to greater light availability. Richness was roughly doubled in high-severity burn interiors due to the persistence of a suite of native species occurring primarily in this habitat. Richness rose with distance into burns, but declined with increasing elevation. Only three of 188 plant species were non-native; these were widespread, naturalized species that comprised $<1\%$ total cover.

Conclusions: These subalpine wildfires generated considerable, persistent increases in plant species richness at local and landscape scales, and a diversity of plant communities. The findings suggest that fire suppression in such systems must lead to reduced diversity. Concerns about post-fire invasion by exotic plants appear unwarranted in high-elevation wilderness settings.

Keywords: Elevation; Exotic species; Plant species richness; Post-fire succession; Southern Rocky Mountains; Timberline; Treeline; Tree seedling; Wilderness.

Nomenclature: USDA, NRCS (2009).

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Introduction

Fire is a central ecological process in high-elevation and high-latitude temperate forests. Variation in wildfire activity generates heterogeneity in forest vegetation across a range of spatial and temporal scales (Romme 1982; Turner et al. 1997; Brown et al. 1999). Within a given burn, variation in pre-fire forest composition and structure, fuel load, and burn severity lead directly to differential tree mortality and, subsequently, to heterogeneity of regenerating forest stands (Stickney 1986; Turner et al. 1997, 1999; Nyland 1998). Following fire, landscape context – including variation in fire severity, size, and distance from burn edge (Agee & Smith 1984; Turner et al. 1997), and tree propagule availability (Lecomte et al. 2005) — may generate variation in patterns of tree regeneration and post-fire plant community composition.

In mountainous terrain, post-fire tree regeneration pattern is further influenced by topographic variation, including landform position (Romme & Knight 1981), aspect (Donnegan & Rebertus 1999), and elevation (Stahelin 1943). Elevation is particularly important in controlling tree species distributions and forest dynamics. In the Rocky Mountains, tree regeneration at moderate elevations is generally dominated by *Populus tremuloides* (aspen) and *Pinus contorta* (lodgepole pine), and can be rapid and prolific (Stahelin 1943; Whipple & Dix 1979; Peet 1981; Veblen 1986). Regeneration is

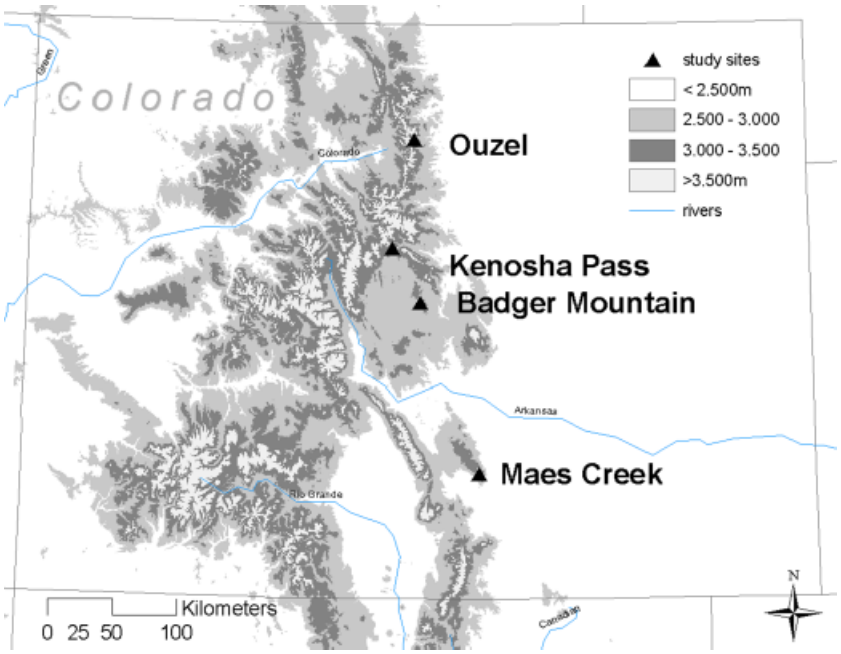

Fig. 1. Locations of study areas in Colorado.

slower at higher elevations, where *Picea engelmannii* (Engelmann spruce) is usually the first to colonize recent burns on mesic sites, followed by *Abies lasiocarpa* (subalpine fir) (Whipple & Dix 1979). On xeric, high-elevation sites, colonization by five-needle pines (*Pinus* subgenus *Strobus*) may be followed by protracted succession to *Picea* and *Abies* (Bates 1917; Rebertus et al. 1991; Baker 1992; Donnegan & Rebertus 1999). Near the alpine treeline, rates of post-fire tree colonization can be extremely low (Stahelin 1943; Billings 1969).

How do patterns of tree regeneration correspond to broader patterns of plant community compositional variation? Environmental factors that control post-fire tree regeneration may secondarily control understory plant community composition and diversity through light availability. In high-latitude boreal forests, transmission of light through the overstory is the single factor most limiting to understory plant productivity and diversity (Hart & Chen 2006). Disturbances such as wildfire that remove the boreal forest canopy lead to rapid increases in productivity and species richness that gradually decline again as the forest canopy develops (DeGrandpré et al. 1993; Rees & Juday 2002). Stand-replacing wildfire in high-elevation subalpine forests would be expected to produce analogous effects on plant communities; however, in mountainous terrain these effects may be magnified by steep topographic gradients. Physical factors that limit tree regeneration (such as elevation, slope, and aspect) may prolong increases in light availability, cover by herbs or shrubs, and the diversity of plant species and communities.

In this research we examine the relationships between environmental factors (including landscape context and topography), tree regeneration, light availability, and plant community composition and diversity in three-decade-old, subalpine burns in Colorado (Fig. 1). Fires in high-elevation forests of the Rocky Mountains are generally severe and spatially extensive but infrequent, with rotation times of ca. 150–400 years (Kipfmueller & Baker 2000; Buechling & Baker 2004; Sibold et al. 2006). Given multi-century fire rotation times, it is unlikely that recent fire suppression over the last century has pushed vegetation composition or structure outside of the range of historical variation in any given stand (Schoennagel et al. 2004). However, fire suppression may have reduced the proportion of high-elevation vegetation that would otherwise be in an early (0–60 years) state of post-fire succession. Recent and expected increases in wildfire activity (Dale et al. 2001; Westerling et al. 2006) and mushrooming fire suppression costs (USDA OIG 2006) suggest that land managers may have to become increasingly strategic in apportioning suppression efforts. An improved understanding of the ecological consequences of past high-severity wildfires may help inform fire management decisions. One period of heightened fire activity that may provide insight into the effects

of high-severity wildfire in the southern Rockies occurred in 1977–1978. Although the total area burned during this period is small by today's standards, many of these fires were considered severe and extensive by the standards of that time (e.g., NPS 1978; Allen 1994).

The primary objectives of this research are to (1) quantify shifts in plant community composition across burn margins, within burns, and along topographic gradients using dissimilarity indices; (2) describe patterns of tree regeneration and their relationships to landscape context and topographic factors, and effects on the light environment in burns; and (3) characterize relationships between landscape factors, topography, light, and plant species richness at local and landscape scales. Finally, we also examine the effects of fire on exotic plant species in high-elevation burns. While post-fire increases in exotic, invasive plants have been well documented in montane forests in the western US (Keeley et al. 2003; Freeman et al. 2007), less is known about the consequences of fire on non-native species in high-elevation forests dominated by *Picea*, *Abies*, and *Pinus*.

Methods

Study locations

We conducted our research in four high-elevation sites that were burned in high-severity wildfires ca. 30 years ago (Fig. 1). From north to south, these are the Ouzel Burn (Ouzel, 1978, Rocky Mountain National Park; 40.2°N, 105.6°W, 2720–3300 m; 436 ha), an unnamed burn near Kenosha Pass (Kenosha, 1977, Pike-San Isabel National Forest; 39.4°N, 105.8°W; 3100–3180 m; 17 ha), the Badger Mountain Burn (Badger, 1978, Pike-San Isabel National Forest; 39.1°N, 105.5°W, 3000–3300 m; 52 ha), and the Maes Creek Burn (Maes, 1978, Pike-San Isabel National Forest; 37.9°N, 105.0°W, 2960–3600 m; 946 ha). Following fire, none of the burns were subject to active rehabilitation efforts (e.g., seeding or replanting). However, evidence for some post-fire salvage logging was present at Kenosha and at the upper elevations of Badger.

All four sites are east of the continental divide in faulted, anticlinal mountain ranges formed during the Laramide Orogeny and underlain by nearly identical geologic substrates: metasedimentary rocks originating 1.8 bya intruded by granite 1.4 bya. The distribution of these burns along a north–south axis (Fig. 1) also provided an opportunity to consider patterns of post-fire succession in relation to the latitudinal variation in forest composition (Peet 1978a; Allen et al. 1991). The general climate of the study area is semi-arid and continental, with precipitation peaking in the spring in the mountains of northern Colorado (Ouzel) but in the late summer farther south, where the influence of the North American Monsoon is stronger. Climate data from lower elevation weather stations near our study sites reflect this pattern (WRCC 2008). Near Ouzel, Allenspark (40.2°N, 105.6°W, 2600 m) has a mean annual precipitation of 53.2 cm (1971–1993) with the wettest month being April (6.5 cm); much of this precipitation occurs as snow in the higher elevations of Ouzel. Below Kenosha Pass, Grant (39.3°N, 105.4°W, 2650 m) recorded 40.3 cm of precipitation annually (1971–2000), with a peak of 6.2 cm in August. 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 summer 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 summer maximum in August (8.6 cm).

Sampling methods

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 elevation bands, and transects were placed across burn perimeters at random within each band; at least one transect was placed in each elevation band. Where burn perimeters within an elevation band covered a wide range of aspects – e.g., where opposite sides of the burn had substantially different ($>90°$) orientations – we further subdivided elevation bands and added randomly placed transects within these divisions. Transects ran perpendicular to the burn perimeter, with five plots spaced along each transect to capture a range of burn conditions. Plots were placed at the partially burned edge where intact forest abutted the burn (0 m), in the burn interior at increasing distances (15, 45, and 100 m), and in the unburned, intact forest (-45 m). Canopy mortality in the burn interior plots was mostly 100%; infrequently plots had only partial canopy mortality.

Between 28 June and 05 September 2007, we sampled 200 plots: 70 plots at Ouzel, 10 at Kenosha, 40 at Badger, and 80 at Maes.

Sample plots were 5×20 m and oriented with the long axis perpendicular to the transect. At plot center, we collected the following data: spatial location (UTM NAD 84 Zone 13) and elevation using a handheld GPS unit with 15 m resolution (Garmin, Olathe, KS), per cent slope (clinometer reading), and aspect (compass bearing). Plots were categorized into three classes of burn severity, defined as follows based on the extent of canopy mortality resulting from fire: *unburned* (intact, undisturbed forest with no canopy mortality or other evidence of 1977–78 fire; we cannot exclude the possibility of some light surface burning during these fires), *partial burn* (stands with incomplete canopy mortality, some living trees that clearly predated the burn, often at the fire edge), and *complete burn* (interiors of high-severity burns where no trees survived). We measured tree basal area (at 1.4 m) with a logger's tape and height (>2.5 cm dbh) with a clinometer, and tallied saplings (>1.5-m tall, <2.5-cm dbh) and seedlings (0.1–1.5-m tall) by tree species. Tree seedlings <0.1 m were not included in our tally. We visually estimated percentage cover using standard cover classes for each vascular plant species that occupied $>0.5\,m^2$ (0.5% of the plot; see Appendix S1); species with cover $<0.5\,m^2$ were not recorded. We estimated percentage ground cover by cryptogams, woody debris, leaf litter, bedrock (>4096 mm), boulders (>256–4096 mm), cobbles (>64–256 mm), gravel (>2–64 mm), and mineral soil (<2 mm). In each plot, we took four digital hemispheric photos of the canopy at a height of 1 m, with one photo point located randomly in each 5×5 m quarter of the plot. Photos were taken during uniformly cloudy or twilight conditions. Plant nomenclature follows USDA NRCS (2008).

Statistical methods

Abiotic variables

Because of the elevational zonation of vegetation shifts with latitude (the elevation of characteristic plant species and communities decreasing slightly with increasing latitude; Peet 1978a; Allen et al. 1991) in the southern Rockies, we examined relationships between vegetation and elevation using both actual (sampled) plot elevations and a latitudinally adjusted measure of elevation. Allen et al. (1991) found that floristically similar vegetation zones declined by 106.6 m per degree of latitude between the Wet Mountains and Rocky Mountain National Park (RMNP), between which all of our samples are located. Accordingly, we adjusted elevations by subtracting 0 m from samples taken at Ouzel (in RMNP), 85 m (106.6 m/° latitude×0.3° latitude) from Kenosha, 117 m (106.6 m/° latitude×1.1° latitude) from Badger, and 245 m (106.6 m/° latitude×2.3° latitude) from Maes. While we utilized latitude-adjusted elevation in the statistical models and tests that follow, we also ran these models with the untransformed elevations in case either approach led to different interpretations. Differences between the two approaches were minor and did not change inferences about elevational effects. Aspect was transformed to a SW–NE index running between 1 and −1, [$Aspect = -\cos(\text{aspect} - 45^\circ)$]. Distance to burn edge was measured as the distance from plot center to intact, unburned forest; these distances were log-transformed. Hemispheric photos were analyzed using the software Hemiview 2.1 (Delta-T Devices, 1999) to calculate a mean value for sky cover (total gap fraction).

Vegetation compositional patterns

To examine patterns of plant community compositional turnover along transects running from unburned forest into burn interiors, we calculated Sørensen (Bray–Curtis) dissimilarity between every pair of plots on each transect using the *ecodist* R package (Goslee & Urban 2007). Sørensen dissimilarity is a measure of compositional differences between plots: low dissimilarity indicates very similar types of vegetation, while high dissimilarity indicates very different kinds of communities. We tested for differences between study areas in the mean dissimilarity scores of each transect. We tested for effects of elevation, aspect, and slope on mean transect dissimilarity using backwards elimination multiple linear mixed effects models. Because dissimilarity varied between study areas (ANOVA $P = 0.048$), we utilized mixed-effects models, which parameterize clustering of observations (in this case, transects were clustered within four study areas) as a random factor. We further examined elevational differences in patterns of vegetation compositional dissimilarity by grouping transects into two elevational categories, upper subalpine (adjusted elevation >3050 m, 20 transects) and lower subalpine (<3050 m, 20 transects).

Tree regeneration

Because our size class data exhibited a clear gap between stems <10 cm dbh (post-1977–1978 regeneration) and stems >10 cm (older trees in intact

stands or burn survivors) we grouped all stems <10 cm to represent recent regeneration, and stems >10 cm to represent residual trees established pre-fire.

To test for relationships between tree regeneration density and predictor variables, we used generalized linear mixed-effects models (glmms) as implemented by the *glmmPQL* function in the R software package. We took advantage of the capacity of glmms to (1) model non-normally distributed response variables (in our case, a Poisson distribution of counts of stems in plots), and (2) account for the clustering of observations (plots within transects within study areas) by modeling each level of nesting as a random effect. We examined environmental correlates of regeneration for all tree species combined and for dominant individual species separately. Burn severity was modeled as a categorical variable with three levels: unburned, partial burn, and complete burn, as described above. Other environmental factors examined included distance from edge, elevation, slope, and aspect. 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 & Lemeshow (2000). Second, we used backwards elimination to identify the generalized linear model (excluding random effects) that minimized the Akaike information criterion (AIC). We then added the random effects (site and transect) to this model, and eliminated any terms that were not significant at $P<0.05$.

Plant richness, cover, and light availability at the 100-m^2 plot scale

To examine patterns of species diversity at the 100-m^2 plot scale, we calculated total species richness, tested for differences between sites and burn severity classes using ANOVA, and compared groups using Tukey's HSD (honest significant difference). Because richness varied significantly between sites, we tested for relationships between species richness (including total plot richness and richness within functional groups including graminoids, forbs, shrubs, and trees) and environmental factors including burn severity class, topographic variables, and distance from burn edge using linear mixed-effects models, with site location and transect as random effects. To test for underlying effects of light availability on richness and cover, we separately tested for effects of total gap fraction on functional group richness and cover with linear mixed-effects models. We also modeled the relationship between light availability and elevation, aspect, and slope using the same method.

Plant richness at the landscape scale: assemblages of unburned, partially burned, and completely burned landscapes

We were also interested in contrasting patterns of total species richness, specificity, and overlap between unburned, partially burned, and completely burned stands. For example, across all samples, were more species encountered in burn interiors than in intact forests? Were these species unique to burns, or were they widespread generalists that were also encountered in unburned stands? Conversely, did plant species of undisturbed forests tend to be restricted to those habitats? To assess these patterns, we first tallied the total number of species across all plots within each burn severity class: 41 plots in unburned stands, 45 plots in partially burned stands, and 114 plots that were completely burned. We also tallied the number of species that were exclusive to each class, those that were shared between two classes, and those that were shared between two classes but were absent from the third. To test whether these sets contained significantly fewer or more species than randomly generated patterns, we conducted a randomization test in R. Plots were reassigned at random (without replacement) to groups of 41, 45, and 114 plots, and counts of species were recalculated for each of the sets described above. We conducted 10 000 randomizations, tallied the number of species in each set, and calculated the proportion of randomized runs that yielded a count that was more extreme (higher or lower) than that observed in the field. Proportions ≤ 0.025 are significant at $\alpha = 0.05$.

Exotic species

We tested for relationships between the incidence of exotic species and environmental factors including burn severity class using a generalized linear mixed-effects model, with a logistic response variable (exotic species present or absent), and spatial nesting of samples (transects within sites) modeled as random effects.

Results

Vegetation compositional patterns

Sørensen dissimilarity within transects varied slightly between geographic locations (ANOVA $P = 0.048$, $df = 3, 36$). Compositional turnover

along transects running across burn margins was greatest at the southern sites, Badger (0.67 ± 0.04; mean $\pm$ SE) and Maes (0.65 ± 0.04) and lower at the northern sites, Kenosha (0.59 ± 0.05) and Ouzel (0.56 ± 0.03). However, only Badger and Ouzel differed significantly (Tukey's HSD $P < 0.05$). Mean transect dissimilarity increased with elevation (for both actual elevation and adjusted elevation, lme $P < 0.05$, $df = 35$), but not slope or aspect. Upper-elevation transects showed higher between-plot dissimilarity than lower-elevation transects (Fig. 3). This difference was most pronounced for dissimilarity between intact forests and burn interiors (e.g., -45–100 m), where transects at high and low elevations reached average values of 0.86 ± 0.03 and 0.73 ± 0.03, respectively. Within transects, between-plot compositional dissimilarity was greatest between intact forests (-45 m) and in burn interiors (15, 45, and 100 m), with values generally between 0.6 and 0.8 (Fig. 3). On any given transect, dissimilarity showed a pronounced increase across the burn edge (0 m).

Tree regeneration

Tree regeneration (defined as stems < 10 cm dbh) ranged between 0 and $> 35\,000$ ha^{-1}, averaging 3166 ± 548 ha^{-1} (mean $\pm$ SE) in unburned plots, 4319 ± 519 ha^{-1} in burned plots with partial canopy survival, and 6668 ± 596 ha^{-1} in plots where canopy mortality was total. High densities of regenerating stems were observed for *Populus tremuloides* (maximum density 17 500 ha^{-1}), which showed the largest increases in regeneration in burns relative to residual trees (Fig. 4). *Picea engelmannii* (max. regen. density 18 600 ha^{-1}) and *A. lasiocarpa* (17 100 ha^{-1}) also showed prolific regeneration; both of these species were common trees of unburned stands. *Pinus contorta* (present only at Ouzel and Kenosha) reached a maximum regeneration density of 10 000 ha^{-1}. Comparatively low densities of regeneration were observed for *Pinus aristata* (max. 1800 ha^{-1}), and *Pinus flexilis* (max. 2700 ha^{-1}) despite the prominence of mature trees of these species in unburned stands (Fig. 4). Other species that occurred as only minor components of the stands sampled included *Abies concolor* (white fir) and *Pinus edulis* (piñon pine) at Maes Creek, *Pseudotsuga menziesii* (Douglas-fir) at Badger and Maes Creek, *Picea pungens* (Colorado blue spruce) at Badger, and *Juniperus scopulorum* (Rocky Mountain juniper) and *Pinus ponderosa* (ponderosa pine) at Ouzel (see Appendix S1 for a complete species list).

Tree regeneration was much greater in burned stands than in unburned stands, with most species showing slight to moderate increases in partially burned plots, and greater increases in completely burned plots (Fig. 4, Table 1). However, for most species, post-fire increases in regeneration were moderated by declines in density with increasing distance into the burned area. *A. lasiocarpa*, *Pinus contorta*, *Picea engelmannii*, and *Pinus aristata* all showed pronounced decreases with distance; only *Populus tremuloides* and *Pinus flexilis* did not exhibit this effect (Fig. 4, Table 1). Topographic factors were also related to regeneration: *Populus tremuloides* regeneration was favored on NE aspects, *Pinus flexilis* on SW aspects, and post-fire *Pinus contorta* regeneration declined on steep slopes.

Overall, tree regeneration in each burn severity class decreased with increasing elevation (Table 1, Fig. 5). This pattern did not hold for all individual species—only *Pinus contorta* and *Populus tremuloides* showed a significant decrease in regeneration, whereas *Pinus aristata* regeneration increased over the elevational range (Table 1). Mixed-effects models showed similar coefficients for either raw elevation data or latitude-adjusted elevation on regeneration for all species. Regeneration density declined with elevation (adjusted to RMNP) most rapidly in high-severity burn interiors, showing similar slopes for Maes, Ouzel, and all sites together (Fig. 5). Regeneration declined more gradually with elevation in partial burns and unburned stands, although the latter regression was not significant (Fig. 5). Extrapolating these regression slopes out to their x-intercepts yields estimates of an upper elevational limit to tree regeneration that is close to the actual elevation of the alpine treeline in Rocky Mountain National Park. Predicted intercepts are 3532 m (complete burns, all sites), 3423 m (complete burns, Maes), 3500 m (complete burn, Ouzel), 3675 m (partial burns, all sites), and 3808 m (unburned, all sites); the elevation of the alpine treeline is around 3500 m, although it may be locally depressed by 100–200 m in some sites because of aspect and topography.

Changes in tree species composition from north to south included a decrease in the abundance of *Pinus contorta*; this species was not present at Badger Mountain or Maes Creek, where aspen, though present at all sites, became more abundant. *Pinus flexilis* was dominant in xeric, subalpine stands at Ouzel, north of the range limit of *Pinus aristata*. *Pinus aristata* was abundant and *Pinus flexilis* was uncommon at Badger Mountain. *Pinus aristata* was abundant only at high elevations at Maes, where

Pinus flexilis was restricted to lower elevations. *A. lasiocarpa* was only encountered at Ouzel.

Plant richness, cover, and light availability at the 100-m^2 plot scale

At the 100-m^2 scale of our sample units, burns contained increased plant species richness to that of nearby, unburned stands (Fig. 2, Tables 2 and 3). Topographic and spatial patterns of richness show several links to those of cover and tree regeneration (Fig. 2, Table 2). Shrubs, forbs, and graminoids all showed increased richness in 30-year-old burns relative to undisturbed stands (Table 3). Models suggest that partial burns increased richness (total richness, and of forbs and graminoids) slightly more than complete burns, but that richness also increased with increasing distance into burns (Table 2). Richness of trees, shrubs, and forbs all declined with elevation, while graminoid richness increased with elevation. Shrub richness was greater on steeper slopes and graminoid richness greater on SW aspects.

Underlying these patterns are relationships between richness, cover, and light availability. Richness of both graminoids and forbs were strongly positively related to their cover (graminoid richness $= 0.08 \times \text{cover} + 1.9$, $r^2 = 0.38$; forb richness $= 0.11 \times \text{cover} + 2.7$, $r^2 = 0.44$; for both, lme $P < 0.001$, 159 *df*). However, neither tree richness nor shrub richness showed this relationship (lme $P > 0.05$, 159 *df*). In turn, both cover and richness of

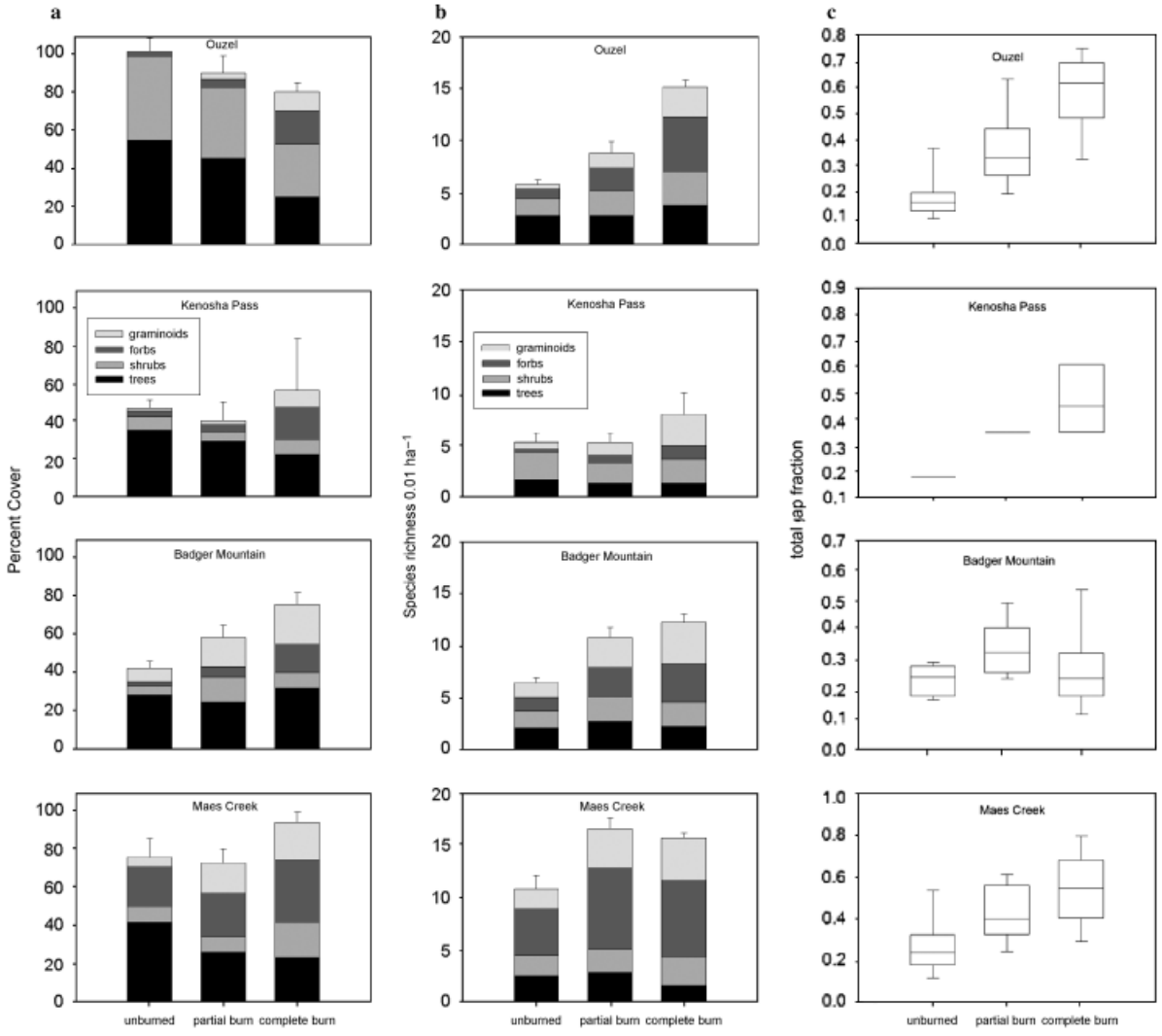

Fig. 2. Cover (**a**) and richness (**b**) by functional groups, and total gap fraction (**c**) in stands that exhibited no evidence of fire (unburned), partial canopy mortality (partial burn), and complete canopy mortality (complete burn) in each study area. Columns represent mean values; error bars represent 1 SE.

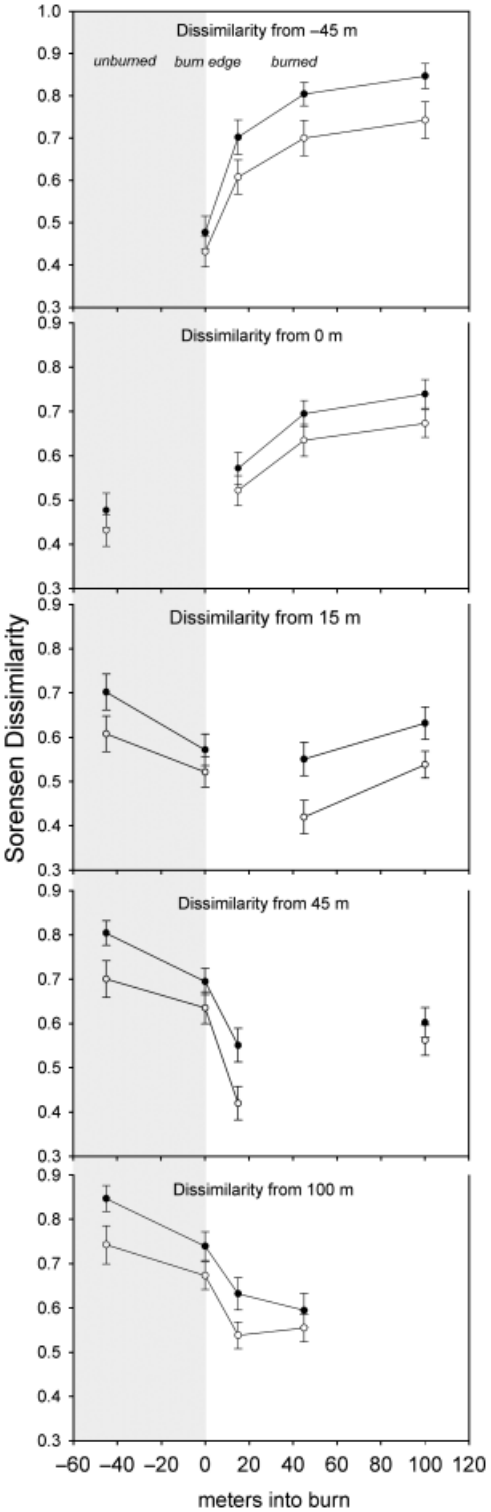

Fig. 3. Mean dissimilarity along transects running from unburned intact forest (plots at −45 m) through the burn edge (0 m), into burn interiors (15, 45, and 100 m). Sørensen distance between each plot and all other plots on the transect is averaged across high-elevation (filled symbols) and low-elevation (open symbols) transects. Error bars represent 1 SE, $n = 20$ for each elevational group.

graminoids were positively related to light availability at 1-m height (graminoid cover = 36×total gap fraction, $r^2 = 0.20$; graminoid richness = 5.7 ×total gap fraction, $r^2 = 0.30$; for both, lme $P < 0.001$, 159 *df*). Likewise, forb cover and richness also showed strong positive relationships to light availability; these relationships only became apparent if elevation was included as a covariate in these models (forb cover = 22×total gap fraction − 0.035×adjusted elevation + 113, $r^2 = 0.12$; forb richness = 8.05×total gap fraction − 0.006× adjusted elevation + 31, $r^2 = 0.30$; for both, lme $P < 0.001$, 158 *df*). Shrub richness showed a similar relationship to gap fraction and elevation (shrub richness = 1.81×total gap fraction − 0.004× adjusted elevation + 14, $r^2 = 0.20$; lme $P < 0.001$, 158 *df*). However, shrub cover and cover and richness of trees did not show similar relationships to light availability (lme $P > 0.05$, 159 *df*).

Light levels at 1-m height showed no relationship to elevation in unburned stands (lme $P > 0.05$, 36 *df*) but were positively related to elevation in partially burned stands (total gap fraction = 0.0004 ×elevation − 0.67, $r^2 = 0.23$; lme $P = 0.008$, 36 *df*). In complete burns, total gap fraction was positively related to both elevation and distance into the burn (total gap fraction = 0.0006×elevation + 0.075×log (distance to burn edge) − 1.41, $r^2 = 0.32$; lme $P < 0.001$, 72 *df*).

Overall, high-severity burn interiors were richer than stands retaining partial canopy cover. However, this pattern appears to shift from northern to southern sites. At Ouzel, unburned and partially burned plots are not significantly different, but complete burns contain significantly more species. There were no significant differences between burn categories at Kenosha (likely due to low power resulting from fewer samples). At Badger and Maes, partially and completely burned plots contained more species than unburned stands but were not statistically distinguishable. Richness was highest in partially burned plots at Maes, which averaged over 16 spp. Maes also stands out as exhibiting greater species richness in each burn severity class than the other sites. Unburned plots there, averaging >10 spp., were particularly rich relative to undisturbed plots at the other study sites.

Plant richness at the landscape scale: assemblages of unburned, partially burned, and completely burned landscapes

Results of our randomization test (Table 4) of counts of all species, exclusive species, and shared

species to burn severity classes illustrate landscape-level patterns of plant richness and composition resulting from fire. Far fewer species (78) occurred in unburned forest relative to that expected based on randomizations of the entire sample (119; Table 4).

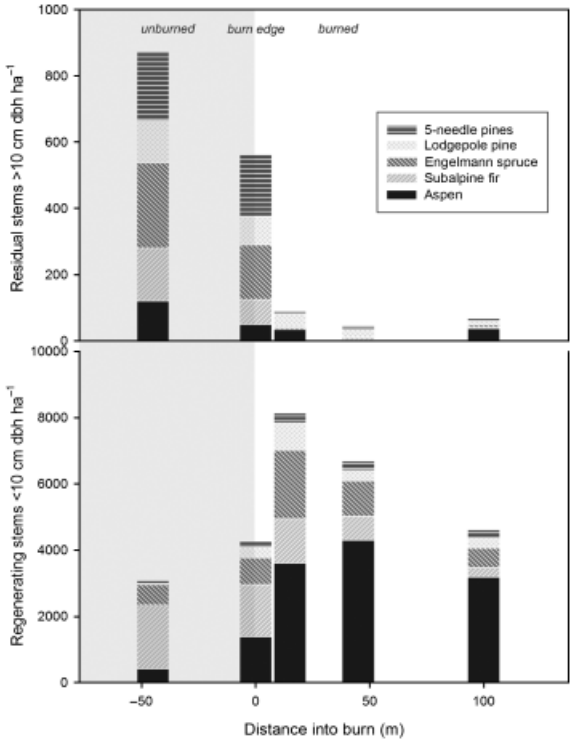

Fig. 4. Densities of residual trees (upper panel) and recent regeneration (lower panel) for dominant tree species, sampled along transects running from unburned (− 45 m) stands through the burn edge (0 m) and at 15, 45, and 100 m into the interiors of 30-year-old burns.

In the high-severity, complete burns, more species (173) occurred than expected (162), although this result was not significant at $\alpha = 0.05$. While the count of species that were restricted to unburned or partially burned habitats did not differ from that generated at random, over a third of the species of complete burns (60) occurred only in this habitat, a count much greater than randomly expected (38). Significantly fewer species than expected were shared between either partial or complete burns and unburned stands, and very few species shared between complete burns and unburned stands did not also occur in partial burns (Table 4). However, a large proportion of the species that were shared between partial and complete burns (44 of 107) were not found in unburned stands (20 species expected).

Exotic species

Of 188 vascular plant species encountered in our sampling, only three were non-native (see Appendix S1 for complete species list). These exotic species were *Taraxacum officinale* (common dandelion), *Poa pratensis* (Kentucky bluegrass), and *Bromus inermis* (smooth brome). Across all samples, foliar cover by these species together was $<1\%$, averaging $0.75 \pm 2.73\%$ (mean $\pm$ 1 SD). Cover was slightly higher in burns: exotics averaged $0.12 \pm 0.78\%$ in unburned plots, $0.22 \pm 0.60\%$ in partially burned plots, and $1.18 \pm 3.51\%$ in completely burned plots. One or more exotic species was encountered in 44/200 (22%) sample plots. Incidence of exotics increased in partially and completely burned stands (glmm $P = 0.006$ and 0.0002, respectively, $df = 158$)

Table 1. Partial regression coefficients for generalized linear mixed-effects models (Poisson regressions) of recent tree regeneration density (stems <10 cm dbh ha^{-1}) for all species combined and for individual species. Burn classes (partial and complete canopy mortality) are categorical variables; these coefficients represent changes in regeneration relative to unburned plots. Distance into burn is the log-transformed distance (m) between the plot center and unburned forest. Aspect is a continuous index running from SW (+1) to NE (− 1), and elevation was adjusted to account for latitude as described in the methods. Blank cells indicate that the term was not included in the best-fitting model as determined by AIC. Degrees of freedom vary between models for different species because plots outside of the geographic distribution of the species were not included in the model (e.g., plots at Ouzel and Kenosha were not used to model *Pinus aristata* response to fire). $^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$, ^{NS}not significant.

Predictor	Tree species						
	All species	*Abies lasiocarpa*	*Picea engelmannii*	*Pinus aristata*	*Pinus contorta*	*Pinus flexilis*	*Populus tremuloides*
	156 *df*	53 *df*	149 *df*	92 *df*	59 *df*	149 *df*	156 *df*
Intercept	9.582^{***}	3.868^{***}	1.302^{***}	-14.415^{***}	19.082^{**}	-1.009^{NS}	17.004^{***}
Partial burn	0.342^{*}	0.200^{NS}	0.343^{NS}	1.038^{***}	2.078^{**}	-0.104^{NS}	1.332^{***}
Complete burn	1.659^{***}	1.927^{**}	2.862^{***}	1.479^{**}	4.813^{***}	0.964^{**}	2.439^{***}
Distance into burn	-0.587^{***}	-1.837^{***}	-1.379^{***}	-0.617^{*}	-1.505^{***}		
Elevation	-0.002^{***}			0.004^{*}	-0.006^{***}		-0.005^{***}
Aspect						0.498^{*}	-0.425^{**}
Slope					-0.0289^{*}		

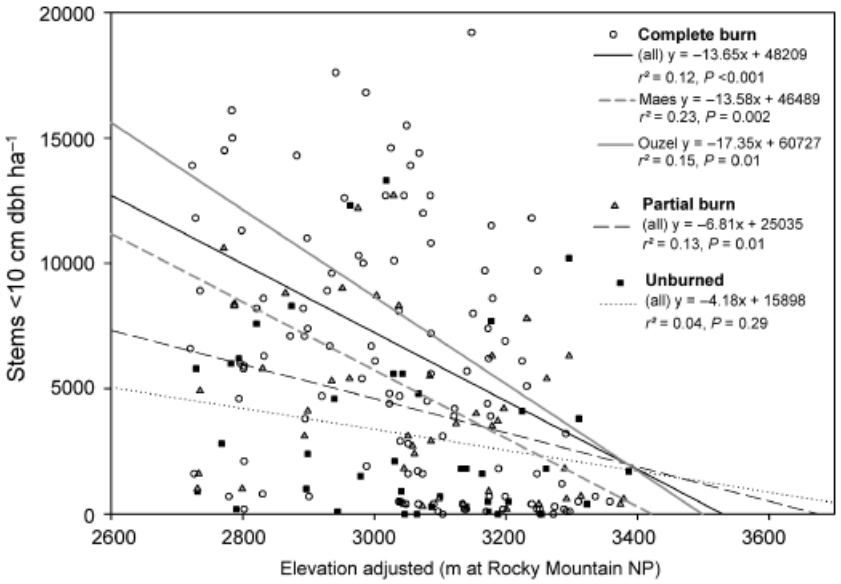

Fig. 5. Recent tree regeneration density (stems <10 cm dbh ha^{-1}) plotted against elevation for each burn severity class. Elevation was adjusted to Rocky Mountain National Park (RMNP) to account for latitude, as described in the Methods. Relationships in complete burns (high-severity burn interiors) are plotted for all sites combined, Maes Creek, and Ouzel. Regression lines are extended beyond the range of our samples to indicate the elevations at which regeneration is predicted to be zero at the *y*-intercept.

Table 2. Partial regression coefficients for linear mixed-effects of environmental predictors of species richness in 100-m^2 sample units. Blank cells indicate that the factor was not retained as significant in the best-fitting model; distance, elevation, and aspect were transformed as described in the methods. $^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$, ^{NS}not significant.

Predictor	Total richness	Tree richness	Shrub richness	Forb richness	Graminoid richness
	156 *df*	159 *df*	156 *df*	156 *df*	156 *df*
Intercept	26.527^{***}	9.474^{***}	9.318^{***}	7.949^{*}	-6.879^{**}
Partial burn	4.298^{***}		0.505^{NS}	2.058^{***}	1.324^{***}
Complete burn	3.699^{**}		1.042^{***}	1.683^{*}	1.064^{*}
Distance into burn	1.799^{*}			0.942^{*}	
Elevation	-0.006^{**}	-0.002^{***}	-0.003^{**}	-0.002^{*}	0.003^{**}
Aspect					0.517^{**}
Slope			0.015^{*}		

Table 3. Species richness by study site and burn severity class ($\pm$ SE). For each column, superscripts indicate significant differences between groups (Tukey's HSD adjusted $P<0.05$). Across rows, letters denote significant differences between burn severity classes within each site. Along columns, numbers identify differences between sites within each burn severity class.

Site	All burn classes	Unburned	Partial burn	Complete burn
All	12.6 ± 0.4	7.8 ± 0.7^{a}	12.2 ± 0.8^{b}	14.5 ± 0.4^{c}
Ouzel	11.9 ± 0.7^{1}	$5.8 \pm 0.5^{a,1}$	$8.8 \pm 1.1^{a,1}$	$15.1 \pm 0.7^{b,1}$
Kenosha	7.6 ± 0.9^{2}	$4.5 \pm 0.5^{a,12}$	$6.0 \pm 1.0^{ab,1}$	$9.2 \pm 0.9^{b,2}$
Badger	10.6 ± 0.6^{12}	$6.4 \pm 0.5^{a,1}$	$10.8 \pm 1.0^{b,12}$	$12.2 \pm 0.8^{b,2}$
Maes	14.9 ± 0.5^{3}	$10.4 \pm 1.3^{a,2}$	$16.6 \pm 1.0^{b,2}$	$15.7 \pm 0.5^{b,1}$

relative to unburned forests. Exotics were found on only in 1/41 (2.4%) unburned plots, but in 7/45 (16%) partially burned plots, and 36/114 (32%) completely burned plots. Frequency of exotic plants was also negatively related to slope (glmm $P = 0.002$, 158 *df*) and tree cover ($P = 0.03$).

Discussion

Three decades after the wildfires of 1977 and 1978, subalpine vegetation exhibited marked compositional and structural shifts across burn edges, including declines in conifer cover, increased cover

Table 4. Observed and expected numbers of species in groupings based on membership in sets defined by burn severity. Groupings reflect the total number of species found in each set, species found exclusively in these sets, species shared between two sets, and species shared between two sets but exclusive to those sets. Mathematical representation follows set theory notation: $a \cup b$, union of a and b (all species found in one or both groups a and b); $a \cap b$, intersection of a and b (number of species that occur in both groups a and b); $a \backslash b$, relative complement of b in a (species occurring in a but not b). Observed # species is that recorded in N sampled plots, expected # of species is the mean number of species in N samples of 10 000 randomized drawings of our dataset. The calculated proportion (P) represents the fraction of randomized trials with species counts as or more extreme than was observed in our samples. For each two-tailed test, proportions <0.025 (in bold) are significant at $\alpha = 0.05$.

Grouping	Mathematical representation	N	Observed # species	Expected # species	P
Total set membership					
Unburned	a	41	**78**	**119**	**0.001**
Partial burn	b	45	116	122	0.285
Complete burn	c	114	173	162	0.037
Exclusive set membership					
Unburned only	$a \backslash (b \cup c)$	41	6	11	0.209
Partial burn only	$b \backslash (a \cup c)$	45	6	12	0.147
Complete burn only	$c \backslash (b \cup c)$	114	**60**	**38**	**0.003**
Shared set membership					
Both unburned and partial burn	$a \cap b$	86	**66**	**91**	**<0.001**
Both unburned and complete burn	$a \cap c$	151	**69**	**104**	**<0.001**
Both partial and complete burn	$b \cap c$	159	107	107	0.471
Shared but exclusive set membership					
Both unburned and partial burn only	$(a \cap b) \backslash c$	86	3	4	0.461
Both unburned and complete burn only	$(a \cap c) \backslash b$	151	**6**	**17**	**0.007**
Both partial and complete burn only	$(b \cap c) \backslash a$	159	**44**	**20**	**<0.001**

and richness of forbs and graminoids, and altered patterns of dominance within each of these layers (Table 1, Figs. 2 and 3). Differences between burned and unburned vegetation grew more pronounced with increasing distance into burns and increasing elevation (Fig. 3). These differences were closely linked with understory light availability and decreased tree regeneration (Figs. 3 and 4), which also declined with increasing distance into burns and elevation.

Across the sampled burns, patterns of tree regeneration exhibited three clear trends: (1) relative to undisturbed sites, burning greatly promoted tree regeneration, but regeneration (2) decreased with increasing distance into burns and away from intact forest, and (3) declined sharply with elevation, particularly in high-severity burn interiors. The highest densities of regeneration were found in high-severity burns proximal to the forest edge at moderate elevations (Fig. 4, Table 1). Regeneration in these sites was dominated by *Populus tremuloides*, which made up a substantial majority of the total regeneration in burns, although it accounted for only a small proportion of both the regeneration and canopy layers of unburned stands. This shift in abundance and the lack of evident declines in regeneration density with distance from the burn edge are consistent with the well-known ecology of *P. tremuloides*, for which seral stands are often initiated by resprouting following stand-replacing fire (Pearson 1914; Baker 1925; Peet 1981). At higher elevations, *Picea engelmannii* dominated post-fire regeneration, consistent with previous studies (Whipple & Dix 1979); *A. lasiocarpa* regeneration also exhibited a positive response to burning although the magnitude of this positive effect was lower than that for spruce (Table 1). *Pinus aristata* and *P. flexilis* exhibited little post-fire regeneration and showed much lower relative abundance in post-fire regeneration than in the canopies of adjacent, undisturbed forests. Although these five-needle pines are typically the first colonizers of xeric, high-elevation sites (Bates 1917; Veblen 1986; Baker 1992; Donnegan & Rebertus 1999), this process may be very protracted, extending far beyond three decades.

Most tree species showed strong declines in density with increasing distance into the burn interior that may reflect lower propagule availability or decreased seedling establishment in an inhospitable environment away from the forest edge (Fig. 4; Table 1). Providing evidence for propagule limitations, only *Populus tremuloides* (a resprouter) and *Pinus flexilis* (which is typically dispersed by Clark's nutcrackers (*Nucifraga columbiana*); Woodmansee 1977) did not exhibit this pattern. *A. lasiocarpa* regeneration density showed steeper declines with distance from burn edges than *Picea engelmannii*, possibly reflecting greater seed mass of the former (USDA 1974). Similarly, following a boreal forest fire, Galipeau et al. (1997) found that *Picea glauca*

became established in the burn interior farther from seed sources, while *A. balsamifera* regeneration was restricted to sites close to seed sources. Interestingly, *Pinus contorta* regeneration density in Ouzel and Kenosha also decreased with increasing distance into high-severity burns; the density of seeds released by fire from serotinous cones should not be negatively affected by distance from unburned stands. This finding suggests that *Pinus contorta* regeneration may be supplemented by propagules from non-serotinous, unburned sources; it may also imply that factors other than propagule availability gave rise to deteriorating regeneration with distance into burn interiors.

Declining tree regeneration with increasing elevation (Fig. 5, Table 1) may be related to (1) shifts from species that regenerate prolifically at lower elevations to species with low reproductive outputs near the alpine treeline, and/or (2) general environmental constraints that depress tree regeneration with elevation. Regeneration densities mirror more general shifts in dominance from *Populus tremuloides* and *Pinus contorta* at the lower end of the gradient, *Picea* and *Abies* in the middle, to *Pinus aristata* near the top. That regression slopes reach the zero intercept at approximately the elevation of the alpine treeline may also suggest abiotic constraints on regeneration that contribute to the generation and/or maintenance of the alpine treeline in the southern Rockies. Cold temperatures may prevent germination (Ferrar et al. 1988) and frost damage, low-temperature photoinhibition, and winter desiccation may impose strong limitations to early seedling growth and survival (Tranquillini 1979; Ball et al. 1991; Germino et al. 2002).

Increasing vegetation compositional dissimilarity with elevation is closely related to decreased tree regeneration and increased light availability. At our lower elevation sites, tree colonization and growth, primarily by *Populus tremuloides* and *Pinus contorta*, increased canopy cover relatively rapidly. Slow development of forest canopies at high elevations permitted a more complete development of open, graminoid- and forb-dominated communities. Paralleling our findings, two other studies reported increasing differences between disturbed and undisturbed communities with increasing elevation, although different processes generated these patterns. In northern Arizona, Fulé & Laughlin (2007) reported greater 1–2 year post-fire changes in the tree layer in high-elevation spruce–fir stands than in low-elevation ponderosa pine stands due to elevational increases in fire severity: fire killed more and bigger trees at high elevation. In southeastern Wyoming, Selmants and Knight (2003) found greater differences between the understories of 30- to 50-year-old subalpine clearcuts and nearby undisturbed stands than between those of clearcut and undisturbed montane forests related to persistent decreases in *Vaccinium* cover and increases by forbs and graminoids following high-elevation disturbance. Taken together, elevational influences on fire behavior and post-fire regeneration may have additive effects. As elevation increases, more severe fire and slower post-fire succession increase the spatial and temporal scales at which fire generates landscape diversity.

High-severity burn interiors exhibited an approximate doubling of understory plant richness (Table 2; Fig. 2), related to light availability, and consisting of a persistent suite of native species that occurred exclusively or primarily in burns, augmented by species characteristic of undisturbed forests. Post-fire increases in plant diversity at the 100-m^2 plot level are consistent with the findings of other studies examining post-disturbance richness across other western North American forests (Selmants & Knight 2003; Huisinga et al. 2005). In high-elevation communities where forest succession is slow, these increases appear to be quite prolonged, and perhaps follow a similar trajectory to high-latitude boreal forests, where understory plant cover and richness may reach a maximum two to four decades after fire, and gradually decline as the canopy redevelops over the next ca. 200 years (DeGrandpré et al. 1993; Chipman & Johnson 2002; Rees & Juday 2002; Hart & Chen 2006). Not surprisingly, trees were the only functional group for which richness at the plot scale was not positively affected by burning; richness is concentrated in the graminoid and forb layers that showed marked post-fire increases (Fig. 2), and richness in these groups was strongly correlated with cover. Total vascular plant richness and forb richness increased with increasing distance into burns, which may also be related to decreasing tree regeneration in these burn interiors. Interestingly, species richness declined with elevation for all groups except graminoids, despite more rapid reforestation at lower elevations. This may be due to differences between the understories of broadleaf and conifer stands at moderate elevations, and the maintenance of a rich forb layer beneath dense *Populus tremuloides* clones (Peet 1978b).

Increased diversity of post-fire communities was pronounced at both the 100-m^2 scale of our sample units and the landscape scale of the entire sample. Sample plots in burns did not simply contain "more

of the same'' generalist plant species that were simply less frequent beneath dense forest canopies. Rather, burns contained a much larger assemblage of species than unburned stands (Table 4). This post-fire species assemblage included a suite of species that were restricted to post-fire communities, as well as a majority of the species that were also found in unburned stands. Whereas plant species encountered in unburned forests were not generally restricted to these undisturbed sites, the flora of burns, especially where high-severity fire resulted in complete canopy mortality, contained many more species that were specific to this habit. Of the 173 species recorded in high-severity burn interiors, over 60% (104; 60 species restricted to completely burned stands and 44 species that also occurred in partially burned stands) did not occur in adjacent unburned forests. The species assemblage we recorded in partially burned stands (burn edges and patches with incomplete canopy mortality) did not contain more species than expected at random. Likewise, at the 100-m^2 plot scale, levels of richness were typically greatest in complete burns and intermediate in partially burned edges, results that are somewhat surprising given the positive effects of edges on plant species diversity (summarized in Ries et al. 2004). Rather than containing a rich assemblage of species of both undisturbed forests and high-severity burns, these communities were essentially transitional between undisturbed stands and high-severity burns in light level and richness, and contained only a subset of the species that occurred in the more open, high-severity burn interiors.

Post-fire patterns of plant community compositional heterogeneity, tree regeneration, and richness appear broadly similar along the latitudinal gradient spanning these burns. However, we found that richness was greatest at our southernmost site, Maes (37.9°N), in the Wet Mountains. The southern sites also appeared to show increased compositional differences between burned and unburned sites, although only Badger showed significant differences from any other site. Allen et al. (1991) reported that the Wet Mountains showed greater plant richness than other study sites in the southern Rockies east of the Continental Divide; they attributed this finding to finer-textured soils. We cannot rule out this hypothesis, as we did not collect data on soil texture. However, plant species richness in many systems is closely linked to precipitation (Hawkins et al. 2003), and the aptly named Wet Mountains appear to receive substantially more precipitation than our other study areas, particularly during the summer months (WRCC 2008).

Exotic plant species were very uncommon in the four burns sampled. We encountered only three non-native species: *T. officinale*, *P. pratensis*, and *B. inermis*. All three of these are widespread naturalized species, and none are considered noxious weeds in Colorado (Swearingen 2006). Only *B. inermis* is listed as invasive in the state (Colorado Weed Management Association 2008), although it is still widely planted for grazing and restoration (Howard 1996). As has been reported from studies conducted in montane forests (Keeley et al. 2003; Freeman et al. 2007), we found positive effects of fire on exotic species. However, the small proportion of the flora represented by these three species ($<2\%$ of the species encountered) and their low cover (collectively, $<1\%$) is in sharp contrast to much higher post-fire increases by exotic species that have been reported from lower elevation ecosystems in the western United States (Crawford et al. 2001; Keeley et al. 2003; Klinger et al. 2006; Freeman et al. 2007). Subalpine settings may be at lower risk of invasion for climatic reasons. The remote, wilderness settings of these burns may also shield them from colonization by exotic plant species: propagule sources are distant, and human visitation and inadvertent dispersal is infrequent.

Conclusions

High-severity fires in southern Rocky Mountain subalpine forests promote substantial diversity at the level of plant species and communities. This diversity is closely linked to the light environment of burns. Concerns that burns will be rapidly colonized by invasive exotic species (e.g., Lynch 2004) appear unwarranted in these subalpine communities; post-fire communities were comprised of a suite of native species that were often found mainly or solely in these burns, augmented by species characteristic of unburned subalpine forests. Tree regeneration in these systems is highly variable and declines with elevation and distance from unburned edges. Reforestation may require decades to centuries in larger, high-elevation burns. In such sites, post-fire increases in plant diversity at local and landscape scales can be pronounced and persistent. Such post-fire diversity – and the paucity of exotic invasive species that we observed – have implications for fire management policies. While wildfire affects a wide range of ecological, economic, and social considerations beyond those discussed here, our findings suggest that successful fire suppression

efforts inevitably yield reductions in the diversity of subalpine plant species and communities.

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References

Agee, J.K. & Smith, L. 1984. Subalpine tree reestablishment after fire in the Olympic Mountains, Washington. *Ecology* 65: 810–819.

Allen, C.D. (tech. ed.). 1994. *Fire Effects in Southwestern Forests*. Proceedings of the Second La Mesa Fire Symposium, Los Alamos, New Mexico, March 29–31, 1994. USDA Forest Service Rocky Mountain Forest and Range Experiment Station. General Technical Report RM-GTR-286.

Allen, R.B., Peet, R.K. & Baker, W.L. 1991. Gradient analysis of latitudinal variation in southern Rocky Mountain forests. *Journal of Biogeography* 18: 123–139.

Baker, F.S. 1925. *Aspen in the central Rocky Mountain region*. U.S. Department of Agriculture Bulletin 1291.

Baker, W.L. 1992. Structure, disturbance, and change in the bristlecone pine forests of Colorado, U.S.A. *Arctic and Alpine Research* 24: 17–26.

Ball, M.C., Hodges, V.S. & Lauglin, G.P. 1991. Cold-induced photoinhibition limits regeneration of snow gum at tree-line. *Functional Ecology* 5: 663–668.

Bates, C.G. 1917. Forest succession in the central Rocky Mountains. *Journal of Forestry* 15: 587–592.

Billings, W.D. 1969. Vegetational pattern near alpine timberline as affected by fire–snowdrift interactions. *Vegetatio* 19: 192–207.

Brown, P.M., Kaufmann, M.R. & Shepperd, W.D. 1999. Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. *Landscape Ecology* 14: 513–532.

Buechling, A. & Baker, W.L. 2004. A fire history from tree rings in a high elevation forest of Rocky Mountain National Park. *Canadian Journal of Forest Research* 34: 1259–1273.

Chipman, S.J. & Johnson, E.A. 2002. Understory vascular plant species diversity in the mixedwood boreal forest of western Canada. *Ecological Applications* 12: 588–601.

Colorado Weed Management Association. 2008. Colorado's Weed List. Available at: http://www.cwma.org/nxwdid.htm (accessed 25 July 2008)

Crawford, J.A., Wahren, C.H.A., Kyle, S. & Moir, W.H. 2001. Responses of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. *Journal of Vegetation Science* 12: 261–268.

Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayers, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J. & Wotton, B.M. 2001. Climate change and forest disturbances. *Bioscience* 51: 723–734.

DeGrandpré, L., Gagnon, D. & Bergeron, Y. 1993. Changes in the understory of Canadian southern boreal forest after fire. *Journal of Vegetation Science* 4: 803–810.

Donnegan, J.A. & Rebertus, A.J. 1999. Rates and mechanisms of subalpine forest succession along an environmental gradient. *Ecology* 80: 1370–1384.

Ferrar, P.J., Cochrane, P.M. & Slatyer, R.O. 1988. Factors influencing germination and establishment of *Eucalyptus pauciflora* near the alpine tree line. *Tree Physiology* 4: 27–43.

Freeman, J.P., Stohlgren, T.J., Hunter, M.E., Omi, P.N., Martinson, E.J., Chong, G.W. & Brown, C.S. 2007. Rapid assessment of postfire plant invasions in coniferous forests of the western United States. *Ecological Applications* 17: 1656–1665.

Fulé, P.Z. & Laughlin, D.C. 2007. Wildland fire effects on forest structure over an altitudinal gradient, Grand Canyon National Park, USA. *Journal of Applied Ecology* 44: 136–146.

Galipeau, C., Kneeshaw, D. & Bergeron, Y. 1997. White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. *Canadian Journal of Forest Research* 27: 139–147.

Germino, M.J., Smith, W.K. & Resor, A.C. 2002. Conifer seedling distribution and survival in an alpine-treeline ecotone. *Plant Ecology* 162: 157–168.

Goslee, S.C. & Urban, D.L. 2007. Ecodist: Dissimilarity-based functions for ecological analysis. R package version 1.1.3.

Hart, S.A. & Chen, H.Y.H. 2006. Understory vegetation dynamics of North American boreal forests. *Critical Reviews in Plant Sciences* 25: 381–397.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach G, G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84: 3105–3117.

Hosmer, D.W. & Lemeshow, S. 2000. *Applied logistic regression*. 2nd ed. Wiley & Sons, New York, NY, US.

Howard, J.L. 1996. *Bromus inermis*. In: Fire Effects Information System. U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available at: http://www.fs.fed.us/database/feis/ (accessed 25 July 2008)

Huisinga, K.D., Laughlin, D.C., Fule P, Z., Springer, J.D. & McGlone C, M. 2005. Effects of an intense

prescribed fire on understory vegetation in a mixed conifer forest. *Journal of the Torrey Botanical Society* 132: 590–601.

Keeley, J.E., Lubin, D. & Fotheringham, C.J. 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecological Applications* 13: 1355–1375.

Kipfmueller, K.F. & Baker, W.L. 2000. A fire history of a subalpine forest in south-eastern Wyoming, USA. *Journal of Biogeography* 27: 71–85.

Klinger, R., Underwood, E.C. & Moore, P.E. 2006. The role of environmental gradients in non-native plant invasion into burnt areas of Yosemite National Park, California. *Diversity and Distributions* 12: 139–156.

Lecomte, N., Simard, M., Bergeron, Y., Larouche, A., Asnong, H. & Richard, P.J.H. 2005. Effects of fire severity and initial tree composition on understorey vegetation dynamics in a boreal landscape inferrred from chronosequence and paleoecological data. *Journal of Vegetation Science* 16: 665–674.

Lynch, D.L. 2004. What do forest fires really cost? *Journal of Forestry* 102: 42–49.

National Park Service (NPS). 1978. *Board of Review Report for the Ouzel Fire, Rocky Mountain National Park*. National Park Service, Rocky Mountain National Park.

Nyland, R.D. 1998. Patterns of lodgepole pine regeneration following the 1988 Yellowstone fires. *Forest Ecology and Management* 111: 23–33.

Pearson, G.A. 1914. The role of aspen in the reforestation of mountain burns in Arizona and New Mexico. *Plant World* 17: 249–260.

Peet, R.K. 1978a. Latitudinal variation in southern Rocky Mountain forests. *Journal of Biogeography* 5: 275–289.

Peet, R.K. 1978b. Forest vegetation of the Colorado Front Range: patterns of species diversity. *Vegetatio* 37: 65–78.

Peet, R.K. 1981. Forest vegetation of the Colorado Front Range: composition and dynamics. *Vegetatio* 45: 3–75.

Rebertus, A.J., Burns, B.R. & Veblen, T.T. 1991. Stand dynamics of *Pinus flexilis*-dominated subalpine forests in the Colorado Front Range. *Journal of Vegetation Science* 2: 445–458.

Rees, D.C. & Juday, G.P. (2002). Plant species diversity on logged versus burned sites in central Alaska. *Forest Ecology and Management* 155: 291–302.

Ries, L., Fletcher, R.J., Battin, J. & Sisk, T.D. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics* 35: 491–522.

Romme, W.H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecological Monographs* 52: 199–221.

Romme, W.H. & Knight, D.H. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. *Ecology* 62: 319–326.

Schoennagel, T., Veblen, T.T. & Romme, W.H. 2004. The interaction of fire, fuels, and climate across Rocky Mountain Forests. *Bioscience* 54: 661–676.

Selmants, P.C. & Knight, D.H. 2003. Understory plant species composition 30–50 years after clearcutting in southeastern Wyoming coniferous forests. *Forests Ecology and Management* 185: 275–289.

Sibold, J.S., Veblen, T.T. & González, M.E. 2006. Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range in Rocky Mountain National Park, Colorado, USA. *Journal of Biogeography* 32: 631–647.

Stahelin, R. 1943. Factors influencing the natural restocking of high altitude burns by coniferous trees in the Central Rocky Mountains. *Ecology* 24: 19–30.

Stickney, P.F. 1986. First decade plant succession following the Sundance Forest Fire, northern Idaho. USDA Forest Service Intermountain Forest and Range Exp. Stn. Gen. Tech. Rep. INT-197. Ogden, UT, US.

Swearingen, J. 2006. WeedUS database, Alien Plant Invaders of Natural Areas. Plant Conservation Alliance, Alien Plant Working Group. Available at: http://www.nps.gov/plants/alien/list/WeedUS.xls (accessed 25 July 2008)

Tranquillini, W. 1979. *Physiological ecology of the alpine timberline*. Springer-Verlag, Berlin, DE.

Turner, M.G., Romme, W.H., Gardner, R.H. & Hargrove, W.W. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecological Monographs* 67: 411–433.

Turner, M.G., Romme, W.H. & Gardner, R.H. 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. *International Journal of Wildland Fire* 9: 21–36.

United States Department of Agriculture, Forest Service (USDA FS). 1974. *Seeds of woody plants of the United States*. Schopmeyer, C. S. (technical coordinator). U.S. Department of Agriculture, Agriculture Handbook 450. Washington, DC, US.

United States Department of Agriculture National Resource Conservation Service (USDA NRCS). 2009. *The PLANTS database*. National Plant Data Center, Baton Rouge, LA, US. Available at: http://plants.usda.gov.

United States Department of Agriculture, Office of Inspector General (USDA OIG). 2006. *Audit Report: Forest Service large fire suppression costs*. USDA, Office of Inspector General, Report No. 08601-44-SF. Washington, DC, US.

Veblen, T.T. 1986. Age and size structure of subalpine forests in the Colorado Front Range. *Bulletin of the Torrey Botanical Club* 113: 225–240.

Westerling, A.L., Jidalgo, H.G., Cayan, D.R. & Swetnam, T.W. 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* 313: 940–943.

Western Regional Climate Center (WRCC). 2008. Western Regional Climate Center. Reno, Nevada. Available at: http://www.wrcc.dri.edu (accessed 25 July 2008)

Whipple, S.A. & Dix, R.L. 1979. Age structure and successional dynamics of a Colorado subalpine forest. *American Midland Naturalist* 101: 142–158.

Woodmansee, R.G. 1977. Clusters of limber pine trees: a hypothesis of plant–animal coaction. *Southwestern Naturalist* 21: 511–517.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Checklist of all plant species sampled and their relative abundances in burn classes in each study area.

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