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# Grassland restoration with and without fire: evidence from a tree-removal experiment

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*Abstract*. Forest encroachment threatens the biological diversity of grasslands globally. Positive feedbacks can reinforce the process, affecting soils and ground vegetation, ultimately leading to replacement of grassland by forest species. We tested whether restoration treatments (tree removal, with or without fire) reversed effects of nearly two centuries of encroachment by *Abies grandis* and *Pinus contorta* into dry, montane meadows in the Cascade Range, Oregon, USA. In nine, 1-ha plots containing a patchy mosaic of meadow openings and forests of varying age (20 to >140 yr), we compared three treatments affecting the ground vegetation: control (no trees removed), unburned (trees removed, slash burned in piles leaving 90% of the area unburned), and burned (trees removed, slash broadcast burned). We quantified changes over 3–4 years in soils, abundance and richness of species with differing habitat associations (meadow, forest, and ruderal), and recruitment of conifers. Except for a transient increase in available N (especially in burn scars), effects of burning on soils were minimal due, in part, to mixing by gophers. Tree removal greatly benefited meadow species at the expense of forest herbs. Cover and richness of meadow species increased by 47% and 38% of initial values in unburned plots, but changed minimally in burned plots. In contrast, cover and richness of forest herbs declined by 44% and 26% in unburned plots and by 79% and 58% in burned plots. Ruderal species and conifer seedlings were uncommon in both treatments. Although vegetation was consumed beneath burn piles, meadow species recovered significantly after three years. Long-term tree presence did not preclude recovery of meadow species; in fact, colonization was greater in older than in younger forests. In sum, temporal trends were positive for most indicators, suggesting strong potential for restoration. Contrary to conventional wisdom, tree removal without fire may be sufficient to shift the balance from forest to meadow species. In meadows characterized by historically infrequent fire, small-scale disturbances and competitive interactions may be more critical to ecosystem maintenance and restoration. Managers facing the worldwide phenomenon of tree invasion should critically evaluate the ecological vs. operational need for fire in ecosystem restoration.

*Key words: ecological thresholds; ecosystem conversion; fire effects; forest encroachment; grassland dynamics; meadow restoration; plant diversity; tree–herb interactions; tree invasions.*

## INTRODUCTION

In many regions of the world, grasslands and other non-forested ecosystems are threatened by encroachment of woody plants (Scholes and Archer 1997, Van Auken 2000). Two factors are often implicated: changes in climate that relax abiotic or biotic controls on tree establishment (Emanuel et al. 1985, Rochefort et al. 1994, Coop and Givnish 2008) and changes in the frequency or intensity of disturbances (fire or grazing) that regulate establishment or survival (Miller and Halpern 1998, Norman and Taylor 2005, Sankey et al. 2006, Coop and Givnish 2007). Moreover, once invasions are initiated, positive feedbacks among trees (or between trees and soils) can reinforce the process of establishment (Miller and Halpern 1998, Halpern et al. 2010). The ecosystem consequences of these invasions can be far-reaching, affecting carbon storage, soil biogeochemistry, and biological diversity (Dye et al. 1995, Hibbard et al. 2001, Jackson et al. 2002, Chapman et al. 2004, Haugo and Halpern 2007). Restoration has thus become a critical management objective where woody plants threaten the ecological functioning of non-forested ecosystems. In this paper we demonstrate that restoration treatments that remove conifers from montane meadows, with or without prescribed fire, can benefit resident meadow species at the expense of forest herbs, substantially altering more than a century of tree influence within several years of treatment. The common

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assumption that fire is ecologically necessary for restoration thus needs to be reexamined.

The boundaries between forests and meadows or other grasslands can be diffuse and dynamic, characterized by periods of stasis, pulses of tree invasion, and periodic disturbances that remove established trees (Norman and Taylor 2005, Coop and Givnish 2007). However, gradual and persistent invasions leading to woodland or forest suggest a fundamental shift in the balance of these processes, e.g., a change in disturbance regime (fire frequency or grazing) that passes an ecological threshold, resulting in a switch in ecosystem state (Walker et al. 1981, Archer 1989, Fuhlendorf et al. 1996, Beisner et al. 2003). Positive feedbacks can accelerate this process (Wilson and Agnew 1992), but may also limit the potential to restore initial conditions (Heisler et al. 2003, Suding et al. 2004, Briggs et al. 2005, Briske et al. 2006). For example, tree invasion can result in local extirpation of grassland species (Gehring and Bragg 1992, Dye et al. 1995, Briggs et al. 2002), but tree removal may not be sufficient for restoration if target species are propagule- or dispersal-limited (Bakker and Berendse 1999, Bisteau and Mahy 2005, Varner et al. 2005). Trees can also modify the biological or chemical properties of soils in ways that favor their ongoing establishment (Belsky et al. 1989, Ingham et al. 1989, Weltzin and Coughenour 1990, Browning et al. 2008). Finally, fuel accumulations associated with tree invasion can alter the effects of fire. In systems typified by frequent, low-intensity fire, higher severity burns can have adverse or unpredictable effects on soils (Johnson and Curtis 2001, Wan et al. 2001) and vegetation (Korb et al. 2004, Pyke et al. 2010), including invasions of exotic species (D'Antonio 2000, Keeley et al. 2003).

Mountain meadows are key landscape elements in the Pacific Northwest (USA), but are undergoing widespread encroachment by conifers. Recent invasions reflect changes in climate, long-term suppression of fire (natural and human ignitions), and release from grazing pressure (Vale 1981, Magee and Antos 1992, Miller and Halpern 1998, Takaoka and Swanson 2008). Locally, loss of montane grasslands has been estimated at >50% since the 1940s (Takaoka and Swanson 2008, Zald 2009). Characteristic of south-facing slopes, ridgetops, and high-elevation plateaus, non-forested habitats comprise a small portion (<5%) of the landscape (Dailey 2007), but contribute disproportionately to the local and regional diversity of plant and animal species (Hickman 1976, Franklin and Halpern 1999). Faced with gradual loss or degradation of these habitats, federal land managers have begun to explore tree removal and prescribed fire as tools for restoration. However, they do so with limited understanding of the historical role of fire, the extent to which meadows have been modified by tree encroachment, and the potential for adverse effects of fire in these highly altered systems.

In this experiment, we assess the responses of a montane meadow ecosystem in the Cascade Range of Oregon to tree removal and prescribed fire following long-term conifer encroachment. We build on previous studies of this system that explore the history of invasion, associated changes in vegetation and soils, and possible barriers to restoration. Encroachment has occurred for nearly two centuries, with a massive wave of invasion in the mid-1900s (Rice 2009, Halpern et al. 2010). As a result, meadow species have been locally extirpated and replaced by forest herbs, including highly clonal species that may limit the potential for recovery (Haugo and Halpern 2007, 2010). Moreover, the soil seed bank lacks most resident meadow species, making reestablishment contingent on seed sources in residual meadow openings. Seed banks are instead dominated by ruderal species (Lang and Halpern 2007), which can be strong competitors in newly disturbed environments. Conversion to forest has also led to significant changes in soil chemical and biological properties, including presence of ectomycorrhizal mats that promote conifer establishment (Griffiths et al. 2005) and reduction in soil disturbance by gophers, which is critical to the structure and dynamics of these meadows (Jones et al. 2008). The potential barriers to restoration are thus numerous.

The manipulation of fire serves two critical purposes in the current experiment: to test the necessity of fire for ecological restoration and to evaluate alternatives for fuel reduction, using treatments that combine tree removal with pile or broadcast burning. Although these meadows may owe their origin and/or maintenance to fire, restoration may or may not require reintroduction of fire. Moreover, broadcast burning may not be desirable if fuel accumulation from forest development or tree removal yields high-severity fires that adversely affect soils or vegetation. Although pile burning is an efficient means of fuel disposal, it too can have adverse local effects. Intense heating can produce highly altered soils, leaving persistent scars that are susceptible to invasion of weedy or exotic species (Covington et al. 1991, Haskins and Gehring 2004, Korb et al. 2004). We exploit these treatments to test the ecological necessity of fire vs. tree removal alone, comparing changes in broadcast burned to unburned areas of pile-burned treatments. Comparable responses would indicate a limited ecological role for fire. We also assess the nature and spatial extent of burn-pile effects to evaluate more fully the ecological trade-offs of broadcast vs. pile burning.

Defining restoration targets or measures of success is challenging in systems severely altered by changes in disturbance regime, exotic invasions, or habitat fragmentation (Suding et al. 2004, Hobbs 2007, Thorpe and Stanley 2011). Ours is a model system for evaluating restoration success: communities of native meadow graminoids and herbs lie in close proximity to, and on similar soils as, conifer-invaded meadows supporting variously aged forests (several decades to >140 yr), with understories dominated by forest herbs. We use changes in the abundance and diversity of meadow and forest

Table 1. Forest structural and understory characteristics prior to tree removal from a forest–meadow mosaic in the Cascade Range of Oregon, USA.

| | Control | | Unburned | | Burned | |
|---|---|---|---|---|---|---|
| Vegetation characteristic | Mean | SD | Mean | SD | Mean | SD |
| Forest structure | | | | | | |
| Tree density (trees/ha) | | | | | | |
| *Pinus contorta* | 160 | 117 | 104 | 85 | 113 | 116 |
| *Abies grandis* | 1220 | 381 | 988 | 111 | 1136 | 498 |
| All tree species | 1468 | 500 | 1151 | 217 | 1329 | 640 |
| Tree basal area ($m^2$/ha) | | | | | | |
| *Pinus contorta* | 4.6 | 3.6 | 3.3 | 2.7 | 3.3 | 3.8 |
| *Abies grandis* | 31.5 | 8.0 | 33.6 | 11.5 | 35.1 | 10.1 |
| All tree species | 38.0 | 7.8 | 38.4 | 12.6 | 42.5 | 9.4 |
| Understory | | | | | | |
| Cover (%) | | | | | | |
| Forest species | 26.5 | 5.8 | 42.3 | 13.9 | 44.9 | 25.2 |
| Meadow species | 56.5 | 16.2 | 29.3 | 6.3 | 32.8 | 27.4 |
| Richness (species/subplot) | | | | | | |
| Forest species | 10.0 | 2.1 | 13.1 | 0.6 | 12.7 | 3.3 |
| Meadow species | 9.7 | 0.9 | 6.8 | 0.7 | 6.9 | 4.0 |

*Notes:* Values are treatment means and standard deviations ($n = 3$). Tree density and basal area are based on stems ≥1.4 m tall.

species as short-term indicators of restoration success. We also consider the potential for adverse effects such as the colonization of ruderal (including exotic) species and conifer seedlings. Ultimately, our experiment is designed to test whether restoration is possible with tree removal, whether fire is necessary, and whether duration of tree influence constrains the potential for recovery. Here, we explore initial (3–4 yr) responses as early indicators of the efficacy of these treatments. We address the following questions: (1) Does tree removal promote the abundance and diversity of meadow species at the expense of forest herbs? (2) Does fire enhance restoration or are there adverse effects of broadcast or pile burning on soils or vegetation? (3) Does the duration of tree influence (forest age structure) affect vegetation responses to treatments?

## Study Area

Bunchgrass Ridge is a gently sloping plateau situated along the western slope of the High Cascades in Oregon (USA). The study area (1350 m elevation) supports a 100-ha mosaic of meadows and coniferous forests of varying size, age, and structure (Table 1), reflecting nearly two centuries of tree invasion (Halpern et al. 2010). Loss of meadow habitat was particularly rapid in the mid- to late-1900s (>50% reduction in area; Rice 2009). Meadows support diverse and well-developed communities of mesic- and dry-site graminoids and herbs (Franklin and Halpern 1999, Haugo and Halpern 2007; Appendix A). Forests are dominated by *Abies grandis* and *Pinus contorta*, with herbaceous understories (Appendix A) that vary in composition with forest age and structure. Meadow species decline rapidly with establishment of *Abies* and are replaced by shade-tolerant forest herbs, which dominate within 60–80 years (Haugo and Halpern 2007, 2010).

Soils are deep (>1.7 m), fine to very fine sandy loams derived from andesitic basalt and tephra deposits with varying amounts of glacially derived rock. They grade from Vitric Melanocryands in open meadows to Aquic Vitricryands in older forests. Soil profiles indicate presence of grassland vegetation for centuries (possibly millennia), even in areas that currently support older trees (D. Lammers, *personal communication*). In areas of open meadow, the burrowing activities of the western pocket gopher (*Thomomys mazama*) contribute to considerable mixing and exposure of mineral soil (Jones et al. 2008).

The climate is maritime, with cool, wet winters and warm, dry summers. At Santiam Pass (1488 m), 17 km to the north, temperatures average –6.9° (minimum) and 0.7°C (maximum) in January, and 6.1° and 27.8°C in July. Annual precipitation averages ~220 cm but is highly seasonal, producing frequent summer drought (data for 1948–1985; Western Regional Climate Center; *available online*).[7] Annual snowfall averages ~11.5 m, resulting in a deep snowpack that can persist into May or early June.

Fire is the primary form of disturbance in this region, but is infrequent at higher elevations in the montane zone (Morrison and Swanson 1990, Weisberg and Swanson 2003). There is no evidence (e.g., fire scars or snags) of moderate- or high-intensity fire in the study area in the last two centuries (Halpern et al. 2010), although low-intensity fire may have been used by Native Americans to maintain open habitats (Burke 1979, Boyd 1999). Sheep grazing may have occurred during the late 1800s and early 1900s, as in much of Cascade Range (Elliot 1946, Johnson 1985), but records

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[7] http://www.wrcc.dri.edu/summary/climsmor.html

of grazing in the study area are lacking in Forest Service archives (Johnson 1985; E. Bergland, *personal communication*). Roosevelt elk, which were historically abundant in western Oregon (Oregon Department of Fish and Wildlife 2003), are common in the study area.

## METHODS

### *Site selection, experimental design, and treatment implementation*

We used aerial photographs (1946–1997) and field reconnaissance to delineate a 16-ha area with both past and recent conifer invasion. We established nine 1-ha (100 × 100 m) experimental plots in June 2003. Each plot contained meadow openings and forest patches of varying age and structure (see Haugo and Halpern 2007, Halpern et al. 2010). Plots were randomly assigned to one of three conditions ($n = 3$): (1) control, no trees removed; (2) unburned, all trees removed and logging residues piled and burned leaving most of the ground surface unburned; and (3) burned, all trees removed and logging residues broadcast burned.

Tree removal occurred in January–February 2006 on deep, compacted snow to minimize soil disturbance. Larger trees were cut with chainsaws and smaller trees with a mechanical faller. Rubber-tired and tracked skidders were used to yard tree boles to an off-site landing. To reduce fuel accumulation, trees were removed with limbs attached (to the extent possible). In unburned plots, slash piles (~2 m tall, 2–4 m in diameter) were constructed by hand in June 2006. Piles were dispersed through each plot in locations not sampled for vegetation (also see *Field methods*). Piles were ignited on 2 November 2006 after an extended dry period and burned to completion (95–100% consumption) within two days. In burned plots, narrow fire lines supplemented by a system of fire hoses were constructed around each plot perimeter. Slash was broadcast burned on 28 September 2006. Fine-fuel loadings (1- to 100-h) averaged 53–69 Mg/ha. Plots burned to completion within 2 h; flame length averaged 1–2 m and consumption of fine fuels averaged 67–87%.

### *Field methods*

*Responses to tree removal and broadcast burning.*—Prior to experimental treatment (June 2003), we established a permanent grid in each of the nine plots to create a system of 10 × 10 m subplots (100 subplots/plot). Edge subplots were treated as a buffer and excluded from vegetation sampling. All remaining subplots ($n = 64$) were sampled in four of the plots (two broadcast burned, two unburned), those used to reconstruct tree invasion history and associated changes in vegetation (Haugo and Halpern 2007, Halpern et al. 2010). In the remaining five plots, alternate subplots ($n = 32$) were sampled. For the unburned treatment, burn piles were restricted to subplot boundaries, thus avoiding areas used for vegetation sampling.

To characterize overstory structure prior to treatment, we calculated density and basal area per subplot using the diameters (dbh) of all live trees $\geq$1.4 m tall. Each subplot (sampling unit) was sampled for vegetation using four 1 × 1 m quadrats spaced at fixed distances. Within each quadrat we quantified (1) cover of mineral soil (bare ground), (2) recent gopher disturbance (cover of mounds and tunnel castings; posttreatment only), (3) cover of each vascular plant species, and (4) density of conifer seedlings (posttreatment only). Ground-surface conditions and vegetation were sampled between early July and mid-August in 2004 (pretreatment), 2007, and 2009. Posttreatment samples represent 2 and 4 yr after tree removal and 1 and 3 yr after broadcast burning.

Soils were collected from 15 randomly selected subplots in each plot in early August 2007 and 2009. For bulk density, one soil core (0–10 cm depth, 137 $cm^3$) was collected from the center of each subplot using a bulk density sampler; litter was first removed from the soil surface. For soil chemistry, cores (0–10 cm depth, 35 $cm^3$) were taken with a tube-type sampler (Oakfield Apparatus, Oakfield, Wisconsin, USA). After removing surface litter, cores were extracted from two points adjacent to each of the four vegetation quadrats; the eight subsamples per subplot were composited as they were collected. On the same day, samples were set out to air dry (<25°C) for ~72 h.

*Local effects of pile burning.*—Burn-pile scars were assessed for changes in soils and vegetation independent of the treatment comparisons. In July 2007 (one year after pile burning) we estimated the cover of burn scars in each plot using the line-intercept method. Ten 80-m transects were run from random points along the southern edge of each plot (inside the buffer). Cover was estimated from the proportion of total transect length intersected by burn scars.

Vegetation was sampled in a random subset of burn scars (10 burn scars per plot, 30 burn scars total) using a design that tested for spatial variation in response. From the center of each burn scar we established a transect in a random direction across the edge of the scar into unburned vegetation. Permanent quadrats (0.2 × 0.5 m) were placed along each transect at four locations: (C) scar center (white ash or reddened mineral soil), (E) burned edge (blackened duff or charcoal), (U1) unburned edge, and (U2) unburned vegetation at a distance from U1 equal to the distance between C and E (0.5–1.7 m). Quadrats were sampled at the same time (posttreatment only), and for the same variables, as in the larger experiment.

Soils were collected from half of the burn scars sampled for vegetation (5 burn scars per plot, 15 burn scars total). One bulk density sample (10 cm depth, 137 $cm^3$) was collected adjacent to quadrats C, E, and U2. Samples for soil chemistry were taken with a tube-type sampler (as before) at six locations adjacent to each quadrat; subsamples were composited as they were collected and were processed as in the larger experiment.

### *Laboratory analysis of soils*

Soil chemistry was analyzed at the University of Washington Analytical Services Center. Air-dried samples were sieved to a <2-mm fraction. For total carbon (C) and nitrogen (N), subsamples were ground and concentrations (percentage dry mass) were determined by dry combustion in a CHN analyzer (model 2400; Perkin Elmer, Shelton, Connecticut, USA). Inorganic N ($NH_4^+$-N and $NO_3^-$-N) was extracted with 2 mol/L KCL (50 mL KCl : 5 g soil); extracts were shaken for 1 h, then filtered (Keeney and Nelson 1982). Concentrations of $NH_4^+$-N and $NO_3^-$-N (mg/kg dry mass) were determined in an autoanalyzer (model 500; O-I Analytical, College Station, Texas, USA); we report the combined concentration as total available N. Soil pH was determined in a 2:1 suspension (10 mL deionized water with 5 g soil) using a PHM 85 pH meter (Radiometer Analytical, Cedex, France).

### *Statistical analyses*

*Defining plant functional groups*.—For comparability with other systems, we focused our analyses on functional groups (sets of species associated with distinctly different habitats and resource environments). We classified species as forest understory ($n = 52$), open meadow ($n = 47$), or ruderal ($n = 13$) (Appendix A), as in previous retrospective studies of this system (Haugo and Halpern 2007, 2010, Lang and Halpern 2007). Although this classification simplifies the distributions of some species, it captures the distinct habitat associations of most. Tree species and taxa not easily assigned to a group ($n = 21$) remained unclassified, but contributed minimally to the vegetation (Appendix A). To assess the contributions of the primary growth forms, forest and meadow species were further classified as grasses, sedges, herbs, or shrubs (Appendix A). Nomenclature follows Hitchcock and Cronquist (1973).

*Responses to tree removal and broadcast burning*.—For each functional group (habitat association × growth form) we first summed the cover of species within each quadrat, averaged these (as well as conifer seedling density) for each subplot, then averaged subplot values for each plot (replicate). Species richness was expressed as the mean number of species per subplot. To account for pretreatment variation among plots (Table 1), analyses of functional group responses were based on differences between pre- and posttreatment values. Analyses of ground-surface conditions, soils, and conifer seedling density were based on posttreatment samples.

To assess effects of treatments on ground-surface conditions, soils, functional group cover and richness, and conifer seedling density (questions 1 and 2), we used repeated-measures analysis of variance. Models included main effects of time, treatment, and a time × treatment interaction. Soil bulk density (sampled in 2007 only) was analyzed with one-way ANOVA. For all response variables, standard diagnostics were used to assess normality and homogeneity of variance (Zar 1999). Conifer seedling density required a log-transformation. Significant ($P \leq 0.05$) treatment effects or time × treatment interactions were followed by pairwise comparisons of means (Fisher's LSD; Zar 1999). Analyses were implemented with the aov function in R version 2.12.1 (R Development Core Team 2010).

To compare compositional responses to treatments (questions 1 and 2), we used nonmetric multidimensional scaling (NMS; Kruskal 1964). NMS was run on a matrix of subplots × times (pretreatment, 2007, and 2009; $n = 1248$) using the cover of species (including conifer seedlings) present in $\geq 5\%$ of samples. Bray-Curtis was used as the distance measure. NMS was initiated from a random starting configuration, run for a maximum of 400 iterations, and rerun up to 40 times (or until an instability criterion of 0.0001 was met; McCune and Grace 2002). The final three-dimensional solution (stress of 16.3) was rotated with principal components analysis (PCA) to maximize the variation explained by the first axis. To simplify the graphical display of treatment responses, we computed the centroid for each experimental unit × time ($n = 27$) and plotted these on the first two axes. NMS was implemented using the metaMDS function of the Vegan version 1.11-0 package in R version 2.12.1 (R Development Core Team 2010).

*Duration of tree influence*.—To test whether duration of tree influence affected responses to tree removal and broadcast burning (question 3), we used subplot-scale data. Individual subplots represented the full range of initial vegetation states (forest age structures), including remnant meadow openings, recent invasions (20–80 yr), and past invasions (>140 yr)—a transition characterized by the progressive replacement of meadow by forest species (Haugo and Halpern 2007). We used initial (pretreatment) cover and richness of forest and meadow species as indicators of these vegetation states, and corresponding posttreatment (2009) values as measures of response. For each response variable, posttreatment values were plotted against pretreatment values (initial vegetation state) and compared to a 1:1 isoline (no change in cover or richness). Values above the line represented increases and values below the line, decreases, with the deviation from the line indicative of the magnitude of response. We used linear regression to test whether regression slopes or intercepts for each treatment differed from the 1:1 line, and from each other. Cover data were log-transformed prior to analysis. Regression analyses were implemented with the lm function in R version 2.12.1 (R Development Core Team 2010).

*Local effects of pile burning*.—The potential adverse effects of pile burning (question 2) were assessed with repeated-measures models (with two exceptions). In all models, plot and burn pile (nested within plot) were treated as random effects, and position (C, E, U1, or U2) as a fixed effect. Models included interaction terms for plot × position and time × position, but the time × plot and three-way interaction were not modeled. For all response variables, standard diagnostics were used to assess normality and homogeneity of variance; log- or square-root transformations were applied as necessary. For analyses of plant cover and richness, the center (C) position was excluded (mainly zero values in year 1). Bulk density (sampled only in year 1) and gopher disturbance (mostly absent in year 1) were analyzed using one-way ANOVA. Significant ($P \leq 0.05$) treatment effects or time × treatment interactions were followed by pairwise comparisons of means (Fisher's LSD). Analyses were implemented with the aov function in R version 2.12.1 (R Development Core Team 2010).

## Results

### Responses to tree removal and broadcast burning

*Ground-surface conditions and soils.*—Tree removal, with or without broadcast burning, had minimal effect on most soil properties (Fig. 1). However, burning did result in significant charring or consumption of fine litter and significantly greater exposure of bare ground (mineral soil) than in unburned plots (Fig. 1a) (also see Appendix B: Figs. B1 and B2). Gopher activity, which increased over time, accounted for most soil disturbance in year 3, but did not differ among treatments (Fig. 1a). Among soil chemical properties, only total available N showed a dramatic, but transient, increase in burned plots (Fig. 1f).

*Plant functional groups.*—Forest species (primarily herbs) declined significantly in cover with tree removal in both unburned and burned plots (Fig. 2a, b). As percentages of initial values (see Table 1), total cover at final sampling was reduced by 44% in unburned plots and 79% in burned plots. Declines in richness were significantly greater in burned plots (Fig. 2e–g). As percentages of initial values, total richness declined by 26% in unburned plots and 58% in burned plots. The vast majority of forest species declined in frequency and cover in both tree-removal treatments (Table 2). In the controls during the same period, forest species increased in total cover by 42% and in total richness by 28% of initial values (Fig. 2, Table 1), with most species increasing both in frequency and cover (Table 2).

Patterns among meadow species were more complex. Initial declines in cover (mainly among graminoids) were highly variable among plots, but did not differ among treatments (Fig. 3a–d). Over time, however, positive (or neutral) responses to tree removal resulted in a significant increase in cover in unburned vs. control plots. As percentages of initial values (Table 1), total cover of meadow species increased by 47% in unburned plots, but did not change in burned plots. Sedges and herbs exhibited large increases in unburned plots: 40% and 82% of initial values, respectively. Most meadow species increased in frequency and cover in unburned plots, but not in burned plots, where a greater number of species declined in cover (Table 2). In the controls, cover of meadow species declined by 33% of the initial value.

Richness of meadow species increased in unburned plots, but showed little change in burned plots (Fig. 3e–g). However, this difference was significant only for grasses (Fig. 3g). As percentages of initial values, total richness increased by 38% in unburned plots (vs. 5% in burned plots); grass richness increased by 92% in unburned plots (vs. 9% in burned plots). In the controls, richness of meadow species increased by 18% of the initial value, with 80% of species increasing in frequency (Table 2).

Ruderal species (both natives and exotics) contributed minimally to the vegetation (Appendix A). Cover averaged <0.2% before treatment and 0.4–0.8% among treatments at final sampling (nonsignificant treatment effect; marginally significant effect of time; $P = 0.073$). Densities of conifer seedlings (mainly *Abies grandis*) were reduced significantly ($P < 0.001$) in unburned and burned plots, and declined over time. Densities were 0.04–0.05 seedlings/m$^2$ at final sampling in treated plots vs. 0.9 seedlings/m$^2$ in controls (data not shown).

NMS revealed considerable variation in species composition among plots prior to treatment (Fig. 4a). Following tree removal, unburned and burned plots had similar patterns of compositional change, although the magnitude of change was greater in burned plots. Individual plot trajectories indicated a shift toward greater importance of meadow species (higher scores on NMS1; Fig. 4b). In contrast, control plots showed small, but consistent changes in composition, indicating a shift toward greater importance of forest species.

*Duration of tree influence.*—Cover and richness of forest species declined in 84–85% of unburned subplots and in 94–96% of burned subplots (Fig. 5a, b). For both measures, the magnitude of decline increased with forest age (regression slopes < 1, $P < 0.001$). Rates of decline in cover were comparable in unburned and burned plots (similar regression slopes; Fig. 5a), but declines in richness were steeper with age in burned plots (significant difference in regression slopes, $P < 0.001$; Fig. 5b). In the controls, cover and richness of forest species increased in 75–76% of subplots, regardless of forest age.

Cover and richness of meadow species increased more often in unburned than in burned subplots (81–84% vs. 49–55%; Fig. 5c, d). Cover frequently declined in subplots with limited tree influence, but increased with forest age, patterns accentuated by broadcast burning (significant differences in regression slopes and intercepts, $P < 0.001$; Fig. 5c). Increases in richness were more common in older forests (slopes < 1, $P < 0.001$), but treatment had no effect on the relationship with age (similar regression slopes; Fig. 5d). In the controls, cover of meadow species declined in 86% of subplots, and to a greater degree in older forests (Fig. 5c). In contrast, richness increased in 88% of subplots, but to a lesser degree in older forests (Fig. 5d).

### Local effects of pile burning

*Ground-surface conditions and soils.*—Burn scars occupied <10% of the ground surface in "unburned" plots.

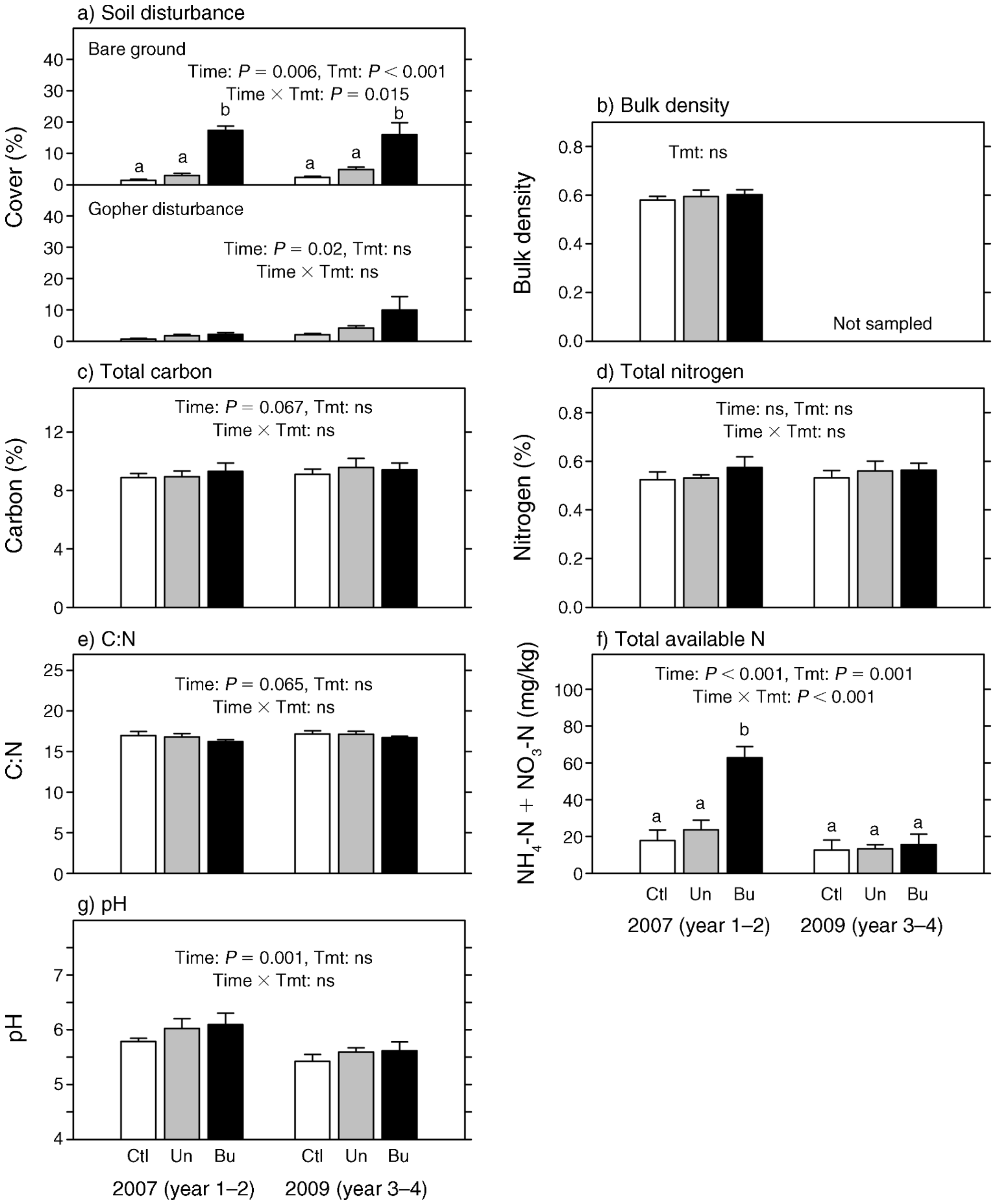


FIG. 1. Measures of (a) soil disturbance and (b–g) soil physical and chemical properties in 2007 (year 1 or 2) and 2009 (year 3 or 4) following restoration treatments (Tmt: Ctl, control; Un, unburned; Bu, burned) in a montane meadow ecosystem in the Cascade Range of Oregon, USA. Values are plot means (+ SE, $n = 3$). Significant ($P \leq 0.05$), marginally significant ($0.05 \leq P \leq 0.10$), and nonsignificant (ns) main effects and interactions are from repeated-measures ANOVA. Lowercase letters denote significant differences among means within years (Fisher's LSD). Bulk density was analyzed with a reduced model (2007 only).

Scar centers (C) were characterized by white ash and mineral soil (bare ground; Fig. 6a) (also see Appendix B: Fig. B3). However, most of the scar (represented by E) was covered by black char (residual litter and small pieces of wood) with significantly less bare ground (Fig. 6a). Gopher disturbance did not vary among positions, but increased over time (Fig. 6a; also see Appendix B: Fig. B4).

Pile burning had small effects on most soil properties. Soil bulk density was not changed (Fig. 6b). Carbon concentrations in the scar center were significantly lower than at U2, but not U1 positions (Fig. 6c). Total N was not reduced in the center, but temporal variation in unburned soils yielded a significant time × position interaction (Fig. 6d). Loss of soil carbon at the center resulted in a small, but significant decline in C:N (Fig. 6e). Burning caused a dramatic spike in total available N (primarily $NH_4^+$-N) at the center, and a smaller (but significant) increase at the edge (Fig. 6f). Concentrations

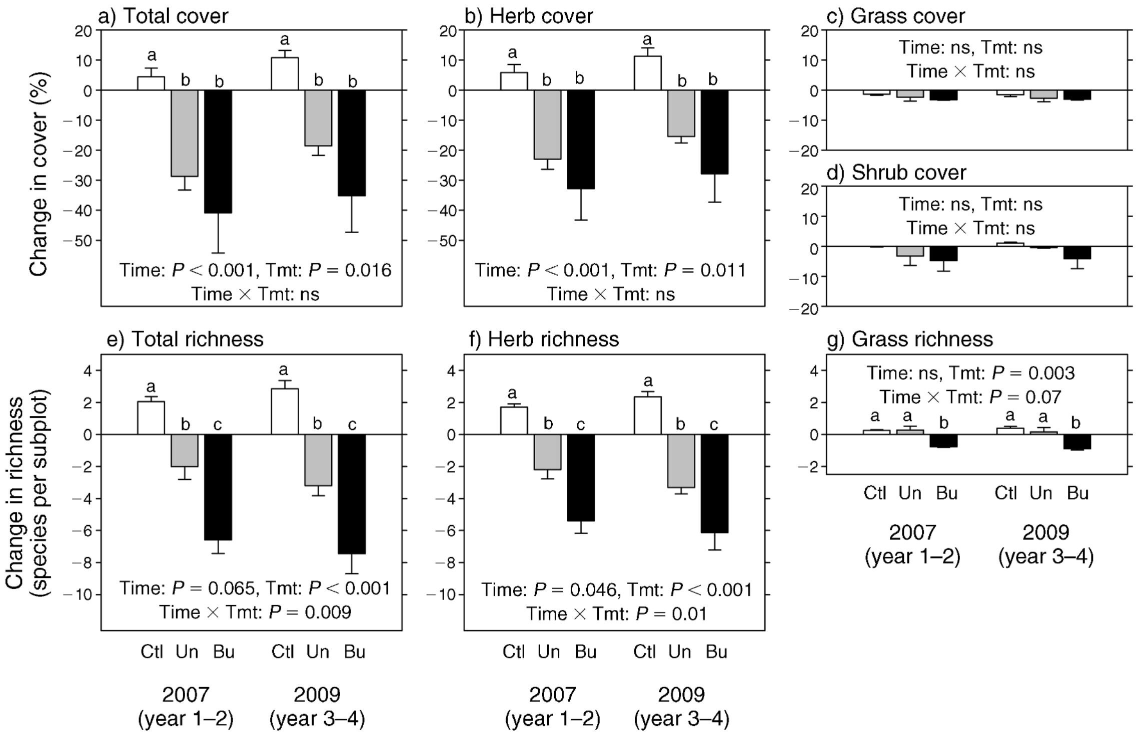


FIG. 2. Responses of forest species (totals and by growth form) to experimental treatments. Values are mean changes in cover (summation of species) or richness (and SE) between pre- and posttreatment values. Growth forms with minimal cover or richness are not presented in separate panels, but are included in functional group totals [panels (a) and (e)]. See Fig. 1 for other details.

declined over time, but remained elevated in the center after three years. Burning also caused a small but persistent increase in soil pH in the center (Fig. 6g).

*Plant functional groups*.—Plant cover was virtually eliminated at the centers of burn scars and greatly reduced at the edges (Fig. 7). By year 3, however, there was significant recovery at the edge for meadow (Fig. 7c, d), but not forest species (Fig. 7a, b). Although center positions could not be analyzed statistically, temporal trends suggest substantial recovery of meadow species (Fig. 7c, d; also see Appendix B: Fig. B3). Ruderal species were rare in burn scars; only three species (two native and one exotic) established in 2.5% of quadrats.

## DISCUSSION

Two centuries of conifer encroachment, culminating in a massive wave of invasion during the mid-1900s, have led to dramatic changes in the extent and quality of meadow habitats at Bunchgrass Ridge. Diverse communities of meadow graminoids and herbs have been displaced by coniferous forests with understories dominated by shade-tolerant forest herbs (Haugo and Halpern 2007). Whether encroachment is a consequence of human influence, or one phase of a natural cyclical

TABLE 2. Percentage of forest and meadow species that increased, decreased, or had no change in frequency or cover.

| | Control | | Unburned | | Burned | |
|---|---|---|---|---|---|---|
| Species | Frequency (%) | Cover (%) | Frequency (%) | Cover (%) | Frequency (%) | Cover (%) |
| Forest ($n$ = 34) | | | | | | |
| Increase | 88.2 | 76.5 | 26.5 | 17.6 | 0.0 | 5.9 |
| Decrease | 5.9 | 20.6 | 73.5 | 82.4 | 97.1 | 94.1 |
| No change | 5.9 | 2.9 | 0.0 | 0.0 | 2.9 | 0.0 |
| Meadow ($n$ = 30) | | | | | | |
| Increase | 80.0 | 43.3 | 73.3 | 63.3 | 46.7 | 40.0 |
| Decrease | 16.7 | 56.7 | 26.7 | 36.7 | 50.0 | 56.7 |
| No change | 3.3 | 0.0 | 0.0 | 0.0 | 3.3 | 3.3 |

*Notes:* Direction of change was based on species' frequency or cover at final sampling (year 3 or 4). The $n$ values in parentheses are the total numbers of forest and meadow species considered and do not include species present in <5% of subplots. See Appendix A for changes in frequency and cover of individual species.

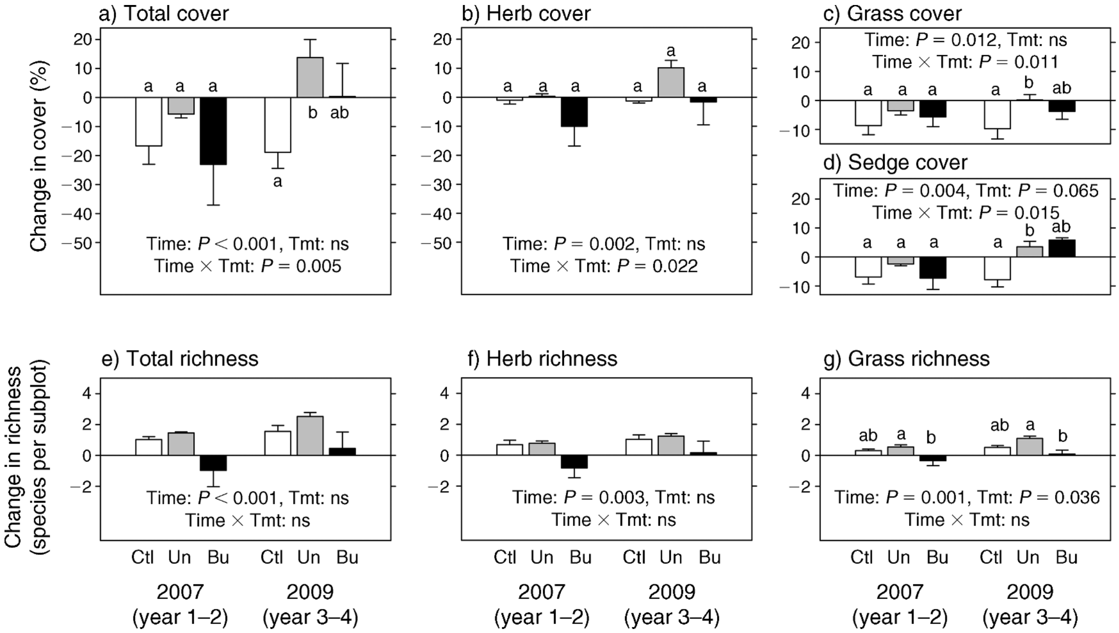


FIG. 3. Responses of meadow species (totals and by growth form) to experimental treatments. Values are mean changes in cover (summation of species) or richness (and SE) between pre- and posttreatment values. See Figs. 1 and 2 for other details.

process (e.g., Wood 1975), the contributions of meadows to the ecological, aesthetic, and recreational values of these mountain landscapes place them as high priorities for conservation and restoration.

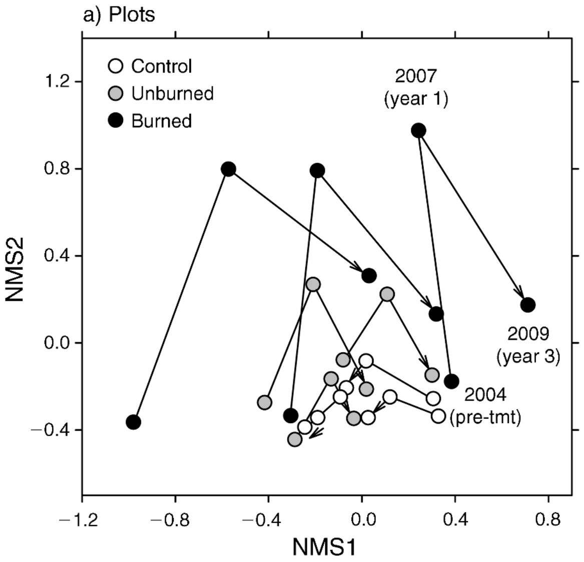
### *Responses to tree removal*

Short-term responses to our experimental treatments suggest strong potential for reversing the effects of decades to well over a century of tree influence. Tree removal resulted in immediate and dramatic shifts in the abundance of species associated with forest and meadow habitats. These changes were even more pronounced relative to controls, where forest species had increased over the study period. In treated plots, most forest herbs showed substantial declines in frequency and cover, even in the absence of fire. Many species showed obvious signs of physiological stress (Lambers et al. 1998), including highly altered growth forms, vertical leaf orientation, thickened leaf surfaces, and early senescence. In combination, these demographic and morphological responses suggest that forest herbs are unlikely to impede the recovery of meadow species adapted to high-light environments.

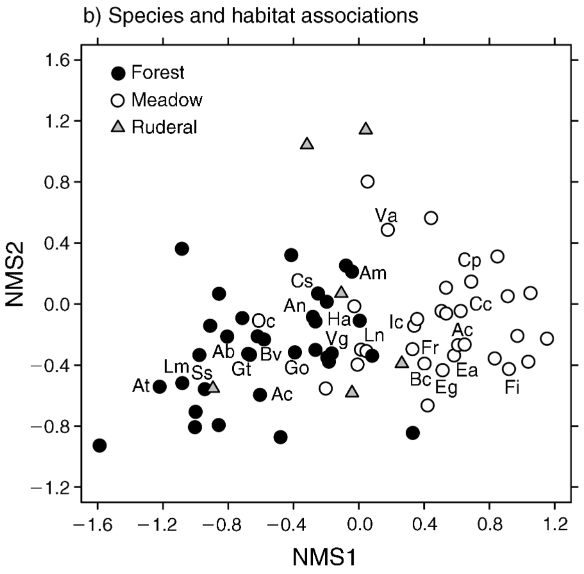
In contrast to forest herbs, meadow species responded positively to tree removal, as anticipated. Net changes in cover and richness were either somewhat positive (unburned plots) or neutral (burned plots). Even among species that declined, frequency decreased very little, with only occasional loss from subplots. Despite the potential for meadow species to respond positively to tree removal, responses were necessarily constrained by low initial frequency (a legacy of long-term tree influence; Haugo and Halpern 2007), and by the absence of most species from the soil seed bank (Lang and Halpern 2007). One notable exception was *Carex pensylvanica*, which increased significantly through a combination of clonal expansion of extant plants and emergence from an abundant seed bank. For the vast majority of species, however, local recruitment required dispersal from residual locations, including remnant meadow openings. Restoration of degraded grasslands is commonly seed limited (Bisteau and Mahy 2005, Lett and Knapp 2005), and species may require artificial reintroduction where degradation is severe (Bakker and Berendse 1999, Foster et al. 2007). In this system, however, sustained increases in the frequency and local diversity of meadow species suggest that natural dispersal has and will continue to enrich the flora. The fine-scale mosaic of forests and remnant meadow openings, which provide source populations near degraded areas, is likely to enhance the potential for dispersal and community reassembly (Eriksson 1996, Muller et al. 1998). In contrast, dispersal limitation may pose a greater barrier to recovery where restoration treatments are applied to larger, more continuous patches of forest.

### *Effects of fire*

Contrary to conventional wisdom, we saw little evidence that fire was critical to reversing the long-term influence of trees in this system. For most measures of response, effects of burning were no different statistically from tree removal alone. Moreover, in our analyses, we did not account for the difference in recovery time between burned and unburned plots (3 vs. 4 yr at final sampling). Had we done so, treatment



a) Plots



b) Species and habitat associations

FIG. 4. Nonmetric multidimensional scaling (NMS) ordination illustrating (a) plot trajectories (centroids of subplots) through time and (b) species by habitat association. Codes are shown for common meadow (M) and forest (F) taxa (those present in ≥50% of subplots with ≥1% cover in at least one treatment × time). Key to abbreviations: Am, *Arenaria macrophylla* (F); Ab, *Adenocaulon bicolor* (F); Ac, *Achillea millefolium* (M); An, *Anemone* spp. (F); As, *Asarum caudatum* (F); At, *Achlys triphylla* (F); Bc, *Bromus carinatus* (M); Bv, *Bromus vulgaris* (F); Cc, *Cirsium callilepes* (M); Cp, *Carex pensylvanica* (M); Cs, *Campanula scouleri* (F); Ea, *Erigeron aliceae* (M); Eg, *Elymus glaucus* (M); Fi, *Festuca idahoensis* (M); Fr, *Fragaria* spp. (M); Go, *Galium oreganum* (F); Gt, *Galium triflorum* (F); Ha, *Hieracium albiflorum* (F); Ic, *Iris chrysophylla* (M); Lm, *Lactuca muralis* (F); Ln, *Lathyrus nevadensis* (M); Oc, *Osmorhiza chilensis* (F); Ss, *Smilacina stellata* (F); and Vg, *Viola glabella* (F).

means would have been even more similar, underscoring the equivocal nature of fire in this system.

As expected, broadcast burning of logging residues resulted in exposure of mineral soil, a common effect of fire in thinned or otherwise untreated forests (Wayman and North 2007, Webster and Halpern 2010). However, the predominance of charred litter indicated low-severity fire. As a consequence, the only substantial change to soils was a transient (first-year) increase in available N. Short-term increases in available N are common after burning of forest residues (Johnson and Curtis 2001, Wan et al. 2001), a product of the combustion of organic matter or increased mineralization (DeBano et al. 1979, Dunn et al. 1979, Pietikäinen and Fritze 1995).

In contrast, pile burning created intense, but localized scarring. Burn scars occupied <10% of the ground surface, but only the centers of scars showed signs of severe burning (reddened mineral soil and white ash). Similarly, effects on soil chemistry were most pronounced at the center. Initially, the concentration of available N was more than twice that of broadcast burned plots and four times that of unburned plots. By year 3, however, available N was markedly reduced— a result of microbial immobilization, plant uptake, or leaching (Antos et al. 2003). These highly localized effects of pile burning are consistent with those described for woodland and forest systems (Covington et al. 1991, Korb et al. 2004), albeit less severe and persistent.

Although reduced burn severity may correlate with comparatively smaller pile size and less intense heating, the rapid healing of burn scars points to a serendipitous, but pervasive, influence on these meadow soils—the tunneling and mounding activities of gophers (Appendix B: Fig. B4). As in other grassland ecosystems (Huntly and Inouye 1988, Reichman and Seabloom 2002), these "ecosystem engineers" play critical roles in processing and redistributing meadow soils. Far less active in the forest, gophers readily disperse into clearings (Ferguson 1999, Verts and Carraway 2000), as evident from the increase in gopher disturbance in tree-removal plots. Mixing of surface and subsurface soils is likely to dampen the effects of fire, and deposition of mineral soil on the surface may benefit plant establishment. Gophers contributed similarly to community reassembly in montane systems buried by volcanic ash (Andersen and MacMahon 1985). More generally, they are integral to maintaining the structure and composition of grasslands—consuming conifer seedlings, burying existing plants, and creating open sites for colonization (Crouch 1971, Ferguson 1999, Reichman and Seabloom 2002, Jones et al. 2008). In sum, tree removal, via its indirect effects on gopher populations, may be far more critical to restoring these herb-dominated ecosystems than any short-term benefit, or adverse effects of, fire.

Both theory (Grime 1979, Thompson 1987) and field observations (Halpern 1988, Halpern and Spies 1995) predict greater development of ruderal species in burned

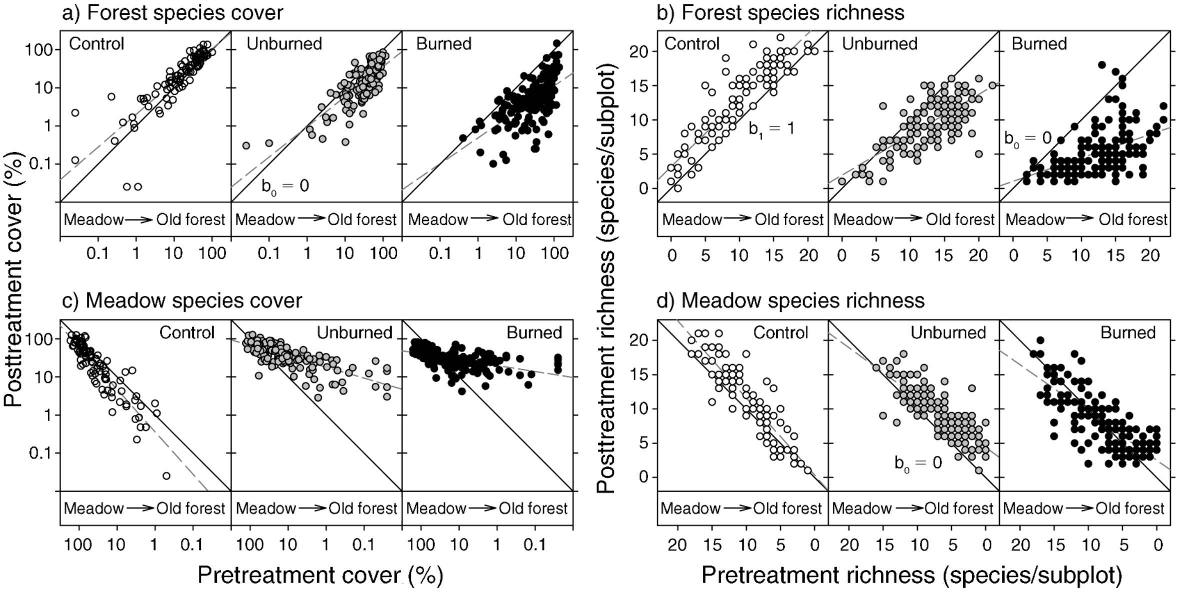


FIG. 5. Relationship between pre- (2004) and final posttreatment (2009) cover (note log scale) or richness of forest and meadow species among subplots representing the gradient from open meadow to old forest (left to right along the *x*-axis). Note the reversed scaling of the *x*-axis for meadow species (high to low values from left to right). Points below the 1:1 isoline represent declines in cover or richness; points above represent increases. Dashed lines are regression lines. Intercepts or slopes that do not differ from the isoline are noted as $b_0 = 0$ and $b_1 = 1$, respectively; all others are significant.

plots, where exposure of mineral soil, heating, and increased N availability enhance their recruitment and growth. However, ruderals were surprisingly sparse in the posttreatment vegetation, given their prominence in the seed bank (Lang and Halpern 2007). Exposure or heating of mineral soil may not have been sufficient in burned plots to promote germination, but heating beneath burn piles probably destroyed most viable seeds (Moore and Wein 1977, Korb et al. 2004). We also anticipated greater recruitment of conifers in burned plots, given the preferential establishment of *Abies grandis* and *Pinus contorta* on mineral substrates (Foiles et al. 1990, Lotan and Critchfield 1990). However, conifer establishment was uniformly low. First-year seedling densities suggested greater germination in burned than in unburned plots, but treatment means did not differ and subsequent mortality was high. *Pinus* seedlings, which are more likely to establish in the open, were uncommon, suggesting dispersal limitation. *Abies*, which has lighter, more readily dispersed seed, may have been limited by drought stress (Foiles et al. 1990), predation by gophers (Ferguson 1999), or reduced access to ectomycorrhizae (Simard 2009). Although current seedling densities suggest limited importance of conifers in the short term, propagule pressure remains high and potential germination sites are plentiful. Future recruitment may be unpredictable or episodic, dependent on the coincidence of an abundant seed year and climatic conditions conducive to germination and survival (League and Veblen 2006).

While burning had only subtle effects on the abundance and diversity of meadow species as a group, effects on taxonomic composition were more substantial. Temporal trajectories in NMS space illustrated considerably greater species turnover in burned than in unburned plots. Two processes can contribute to this effect. Susceptibility to fire varies in relation to the type or depth of perennating structures, resulting in differential loss of species (McLean 1969, Rowe 1983, Halpern 1989, Pyke et al. 2010). For example, the dominant bunchgrass, *Festuca idahoensis*, is vulnerable to fire due to its compact growth form and shallow meristems (Conrad and Poulton 1966, Antos et al. 1983). In this system, *Festuca* was lost from ~50% of burned subplots, but increased by a similar amount in the absence of fire (Appendix A). Alternatively, fire can promote differential establishment via effects on seed beds and associated resource conditions. For example, the native thistle, *Cirsium callilepes*, showed substantially greater recruitment and growth in burned than in unburned plots (Appendix A). Fire can thus leave an imprint on the taxonomic composition of the vegetation. However, this is likely to be of secondary importance to restoring functional composition (abundance and diversity of meadow species), which was responsive to tree removal, but not to fire.

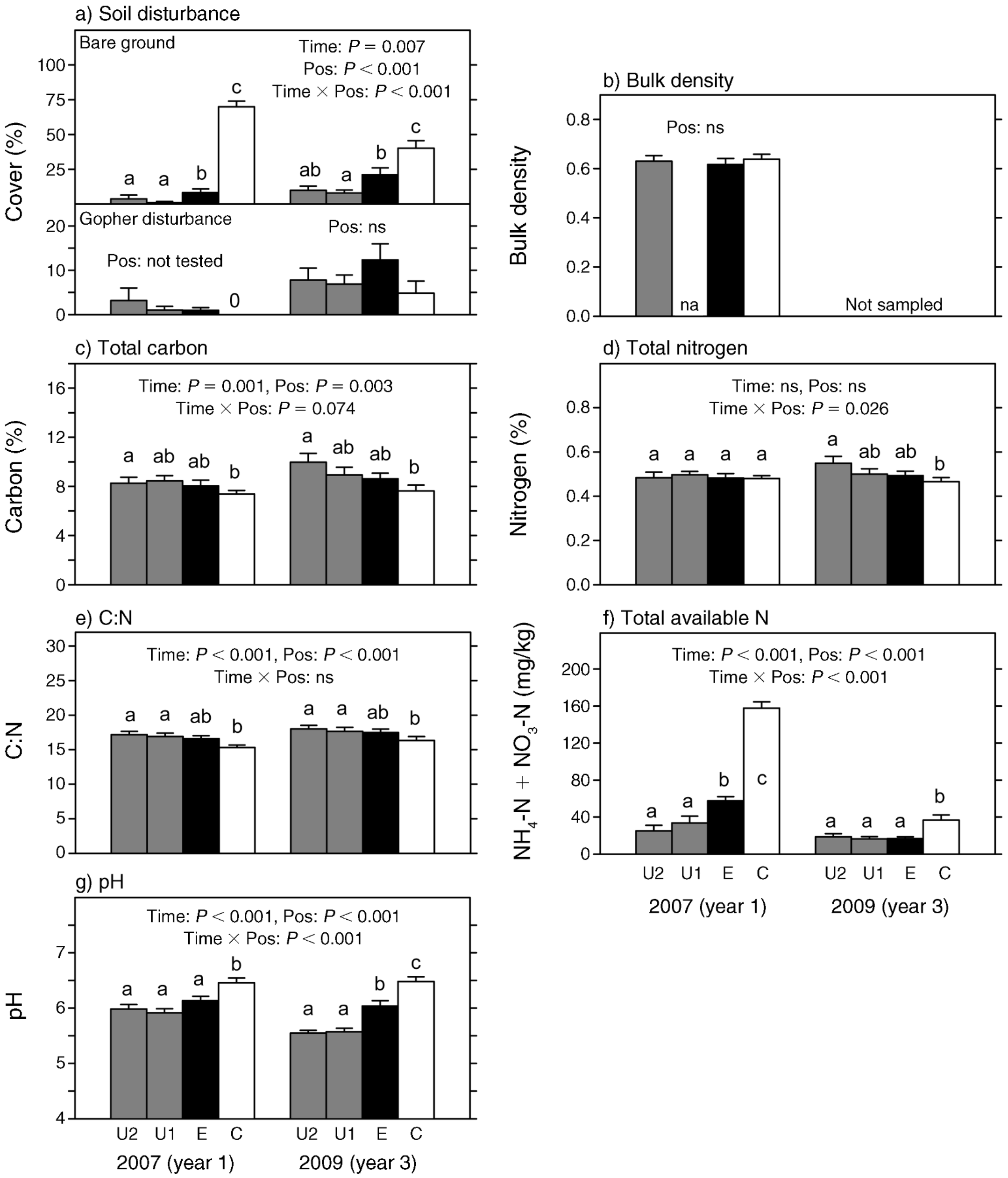


FIG. 6. Ground-surface and soil characteristics in and adjacent to burn scars in 2007 (year 1) and 2009 (year 3). Sample positions (Pos) are: C, center of burn scar; E, burned edge; U1, unburned edge; and U2, unburned, distant from edge. Values are means (+SE) of 15 burn scars. Significant ($P \leq 0.05$), marginally significant ($0.05 < P \leq 0.10$), and nonsignificant (ns) main effects and interactions are from repeated-measures ANOVA; effects of plot × position are not reported (all ns). Lowercase letters denote significant differences among means within years (Fisher's LSD). Reduced models were implemented for (a) gopher disturbance, 2009 (year 3) only; and (b) bulk density, U2, E, and C in 2007 (year 1) only.

### *Duration of tree influence and the potential for restoration*

We saw no evidence of a threshold or switch in ecosystem state that limited the potential for restoration (Wilson and Agnew 1992, Muradian 2001, Suding et al. 2004). Analyses of subplot-scale responses suggest recovery from a broad range of initial vegetation states (forest age structures). In fact, reductions in forest herbs and increases in meadow species were greater in older than in younger forests, trends that were often accentuated by fire. For forest species, greater declines in older forests may relate to a combination of factors: higher initial cover and diversity, thus greater potential for loss; greater representation of late-seral taxa that are more sensitive to fire or abiotic stress (Halpern 1989,

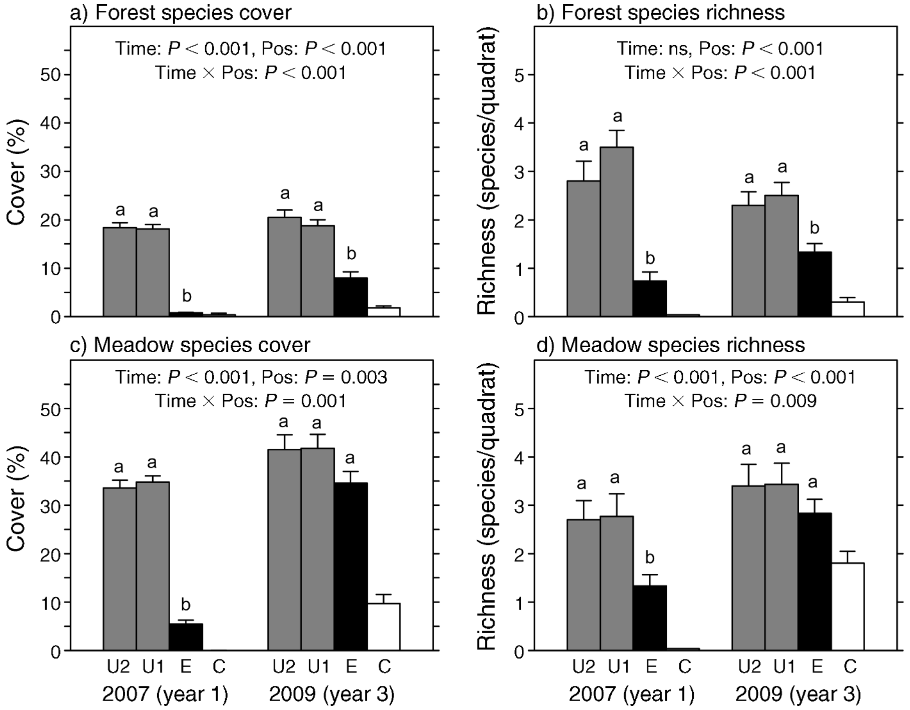


FIG. 7. Cover and richness of (a, b) forest species and (c, d) meadow species in and adjacent to burn scars in 2007 (year 1) and 2009 (year 3). Sample positions are: C, center of burn scar; E, burned edge; U1, unburned edge; and U2, unburned, distant from edge. Values are means (+SE) of 30 burn scars; see Fig. 6 for other details. The center position was not included in ANOVA models (see *Field methods: Local effects of pile burning*).

Halpern and Spies 1995, Halpern et al. 2005); and, in burned plots, increased fire severity due to greater accumulation of fuel (Mitchell et al. 2009). For meadow species, greater increases in richness (recruitment) and cover (growth) in older forests underscore both the sufficiency of dispersal, and the lack of edaphic constraints related to long-term tree influence. Broadcast burning did not enhance (or reduce) rates of recruitment. Thus establishment is likely to be limited more by dispersal than by the characteristics of microsites (Eriksson and Ehrlén 1992, Foster et al. 2004). In contrast, burning did enhance cover of meadow species in older forests, possibly by reducing competition from forest herbs.

Despite the benefits of tree removal for recovery of meadow species as a group, large differences still separated recovering from reference (remnant meadow) communities. Many treated subplots supported a small fraction of the richness and cover of reference communities, and some characteristic meadow species remained underrepresented, limited by low seed production or dispersal (e.g., Kirkman et al. 2004). However, after centuries of tree influence, it is not surprising that additional time would be needed to assess whether tree removal is adequate (or if fire is also necessary) to fully restore the composition, structure, and functioning of these systems.

### *Ecological and management implications*

Conversion of grasslands to woodlands or forests is an important aspect of global change biology. It represents a fundamental physiognomic transformation accompanied by profound ecological changes. The causes of woody-plant encroachment vary regionally and globally, and can include complex interactions among climate, disturbance, and land use. In the current study, we do not address the causes of encroachment, but explore the potential to reverse its consequences, with the goal of restoring the structure and diversity of native montane grasslands. Experiments that test both the methods for reversing the effects of encroachment and the contexts in which restoration is possible are critical given the vast areas of grassland that have undergone similar transformations.

It is commonly assumed that fire is fundamental to maintaining the open nature of grasslands and thus is critical to restoring systems invaded by woody plants. Our study challenges the generality of this assumption. For this common western North American grassland, our experiment indicates that fire (broadcast burning) is not necessary to reverse the effects of decades to multiple centuries of forest influence. Tree removal alone is sufficient to cause a significant shift in dominance from forest understory to meadow species. If the principal contribution of fire is to prevent tree establishment in grasslands or meadows, mechanical removal of trees (preferably at an early stage in the invasion process) may be a simple alternative. Nevertheless, we found that broadcast burning did not adversely affect soils or recovery of meadow species, suggesting that once trees are removed, low-intensity fire could be used to maintain these open habitats. Burning is necessary, however, from a management perspective, to dispose of logging residues, thus reducing future fire hazard. It also removes woody debris that would otherwise shade the ground surface, creating conditions that benefit forest herbs and inhibit meadow species.

Despite the generally positive outcomes of these experimental treatments, tree removal and burning pose numerous logistical challenges. In this mountain ecosystem, felling and yarding were conducted on deep, compacted snow to minimize soil disturbance. Similar operations are not possible at lower elevations. Moreover, climate warming could reduce the range of environments in which logging on snow is possible. Soil disturbance can be reduced by other methods of yarding (e.g., use of suspension cables, rubber-tired skidders, or armoring of extraction routes with woody residues; Miller and Sirois 1986, Wood et al. 2003). To our knowledge, however, these approaches have not been tested on meadow soils.

There are also well-known trade-offs among methods of fuel disposal. Broadcast burning is contingent on weather conditions, and containment costs can be high. Pile burning can be scheduled when fire risk and containment costs are low, but it requires labor-intensive redistribution of fuels. In addition, burn piles can leave persistent scars that serve as foci for invasion and spread of ruderal taxa (including exotics). In this system, however, we found that these scars were transient features, mitigated by gopher disturbance and rapidly colonized by native meadow species. Ultimately, the selection of fuel-reduction methods may not be determined by ecological criteria, but by local operational or economic constraints (Hartsough et al. 2008).

A fundamental challenge in restoration ecology is to determine the relevance of structure vs. process (disturbance in particular) in achieving the goals of restoration (Stephenson 1999, Allen et al. 2002). Although reestablishing historical disturbance regimes may be an explicit goal of restoration, reintroducing natural disturbance processes can be problematic in highly altered landscapes (Suding et al. 2004, Briggs et al. 2005). For example, fire has the potential for adverse effects if exotic species are present that can exploit the conditions created by burning (D'Antonio and Vitousek 1992). Moreover, increasing fire frequency may have little effect on established woody plants that are resistant to burning (Heisler et al. 2003, Briggs et al. 2005). Even in grasslands historically maintained by fire, alternative treatments (e.g., mowing or application of herbicides) may be as effective as fire in restoring native communities, if they modify resource environments in ways that are beneficial to the target species (MacDougall and Turkington 2007). Tree removal appears to serve this function in our experimental system, by exposing forest understory species to stress and enhancing light availability for meadow species. Fire does not appear necessary for reestablishment of meadow species, at least in the short term and at the spatial scales tested. Similar outcomes are likely in grassland ecosystems in which the resource conditions associated with woody-plant removal (rather than the direct effects of disturbance itself) are the principal determinants of community structure. The results of our tree-removal experiment suggest that, once these conditions are met, the principal constraints on meadow recovery are the proximity of seed sources and the dispersal abilities of target species. They also illustrate the potential for tree removal to have indirect or cascading effects via other trophic levels, namely, burrowing animals, whose soil-disturbing activities are fundamental to the structure and dynamics of grasslands and prairies throughout North America.

In highly altered ecosystems, the presence of ecological thresholds and positive feedbacks can pose barriers to restoration (Suding et al. 2004). Although long-term encroachment of woody plants may lead to highly recalcitrant states in some grassland systems (Archer 1989, Heisler et al. 2003, Briggs et al. 2005), our experiments provide clear evidence of the feasibility of restoring meadows from a broad range of forested states, including those in which trees have been present for well over a century. In sum, restoration of this system is a viable possibility, even after conversion to forest. Moreover, managers need not be constrained by the perceived necessity to reintroduce fire as a natural disturbance process. Tree removal alone was sufficient in our system and should be entertained as an alternative in other ecosystems.

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## Supplemental Material

### Appendix A

Mean frequency and cover of plant species observed in the three experimental treatments in 2004 (pretreatment), 2007 (1–2 yr), and 2009 (3–4 yr) (*Ecological Archives* A022-027-A1).

### Appendix B

Photographs illustrating posttreatment conditions in burned (broadcast) and unburned (pile-burned) plots, recovery of burn-pile scars, and gopher disturbance (*Ecological Archives* A022-027-A2).