



# Past tree influence and prescribed fire exert strong controls on reassembly of mountain grasslands after tree removal

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**Abstract.** Woody-plant encroachment represents a global threat to grasslands. Although the causes and consequences of this regime shift have received substantial attention, the processes that constrain reassembly of the grassland state remain poorly understood. We experimentally tested two potentially important controls on reassembly, the past influence of trees and the effects of fire, in conifer-invaded grasslands (mountain meadows) of western Oregon. Previously, we had reconstructed the history of tree invasion at fine spatial and temporal resolution. Using small subplots (10 × 10 m) nested within larger (1-ha) experimental plots, we characterized the fine-scale mosaic of encroachment states, ranging from remnant meadow openings (minimally altered by trees) to century-old forests (lacking meadow species). Subsequently, we removed trees from six plots, of which three were broadcast burned and three remained unburned (except for localized burn piles). Within each plot, subplots were sampled before and periodically after tree removal to quantify the individual and interactive effects of past tree influence and fire on grassland community reassembly. Adjacent, uninvaded meadows served as reference sites. “Past tree influence” was defined as the multivariate (structural or compositional) distance of subplots to reference meadows prior to tree removal. “Reassembly” was defined as the distance, or change in distance, to reference meadows at final sampling. Consistent with theory, we observed greater reassembly of plant community structure than of composition, as loss of meadow specialists was offset by establishment of disturbance-adapted meadow generalists of similar growth form. Nevertheless, eight years after tree removal, most subplots remained structurally and compositionally distinct from reference meadows. Furthermore, fire had both destabilizing and inhibitory effects: it reduced survival of meadow specialists across the range of encroachment states and, where past tree influence was greater, it stalled reassembly by promoting expansion of a highly competitive native meadow sedge. The slow pace of reassembly, despite abundant open space, suggests strong seed limitation: a condition exacerbated by burning. We present a novel test of the importance of past tree influence and fire for restoration of tree-invaded grasslands, offering insights into how constraints on community reassembly vary along a continuum of tree-altered states.

**Key words:** community convergence; conifer encroachment; ecological restoration; grassland restoration; legacy effects; prescribed burning; priority effects; regime shift; woody-plant invasion.

## INTRODUCTION

Ecological systems can undergo regime shifts: transitions in state that have profound implications for biological diversity, ecological processes, and ecosystem services (Scheffer et al. 2001, Folke et al. 2004, Isbell et al. 2013). The processes that lead to these changes in state are well understood and include both external

drivers (climate or disturbance) and internal dynamics (biotic interactions) that can move a system past a critical threshold (Holling 1973, Beisner et al. 2003, Scheffer and Carpenter 2003, Mayer and Rietkerk 2004, Bestelmeyer et al. 2011). However, the factors that limit reassembly of the original state are poorly understood, resulting in significant challenges to restoration science. For example, interventions designed to reverse the effects of a regime shift may lead to undesirable or unintended outcomes: little change (if internal feedbacks confer resilience on the altered state; Holling 1973, Leadley et al. 2014); partial reassembly of the desired state (if target species are seed limited; Damschen et al.

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2008, Brudvig 2011); or development of an alternative, undesired state (if native species are replaced by exotic species; Mayer and Rietkerk 2004, Suding et al. 2004, Hobbs et al. 2006, Suding and Hobbs 2009).

Woody-plant encroachment, a regime shift of global significance, affects grasslands across a variety of biogeoclimatic zones (arid and semiarid grasslands to montane and subalpine meadows; Scholes and Archer 1997, Van Auken 2000, Coop and Givnish 2007, Ratajczak et al. 2012, Weigl and Knowles 2014, Archer et al. 2017). Its consequences include changes in the physical structure of vegetation; loss of biodiversity; habitat fragmentation; altered cycling of carbon, water, and nutrients; and changes in land use (Jackson et al. 2002, Knapp et al. 2008, Barger et al. 2011, Eldridge et al. 2011, Ratajczak et al. 2012). The shift from herbaceous to woody dominance has been attributed to changes in extrinsic factors (e.g., climate, CO<sub>2</sub>, or disturbance regimes) that alter the competitive balance among species (Archer et al. 1995, 2017, Hoch et al. 2002, Briggs et al. 2005, Van Auken 2009). Once woody species establish, however, strong internal feedbacks can accelerate the process, favoring further establishment and persistence (Archer et al. 1988, D'Odorico et al. 2010, Ratajczak et al. 2011), even when climatic conditions are not optimal (Miller and Halpern 1998, Halpern et al. 2010). The shift to woody dominance of once-stable grasslands is particularly striking in the Pacific Northwestern region of the United States, where recent encroachment of conifers threatens the persistence of mountain meadows (Magee and Antos 1992, Miller and Halpern 1998, Zald 2009). For example, in the western Cascade Mountains of Oregon, meadows that occupied 5% of the landscape in 1940 now occupy less than one-half of that area (Dailey 2007, Takaoka and Swanson 2008). Despite their limited and declining distributions, meadows contribute disproportionately to local and regional diversity (Hickman 1976, Franklin and Halpern 1999). Heightened concern among federal land managers over the pace and consequences of meadow loss have spurred interest in reversing the effects of encroachment (e.g., through tree removal or fire) and in testing the contexts in which restoration is possible.

Woody plants, by virtue of their stature and longevity, can significantly alter grassland vegetation and soils (Amiotti et al. 2000, Köchy and Wilson 2000, Griffiths et al. 2005, Haugo and Halpern 2007, 2010). Even if woody species can be removed, subsequent reassembly of the grassland state can be inhibited by “legacy effects”: the influence of past conditions on current processes (Lett and Knapp 2005, Corbin and D'Antonio 2011, Hamman and Hawkes 2013). These effects include an impoverished species pool (Helsen et al. 2013, Coffey and Otfinowski 2018), habitat fragmentation that impedes dispersal (Dzwonko and Loster 2007), persistent changes in soils (Facelli and Brock 2000, Ludwig et al. 2004, Helsen et al. 2016), and preemption of space or resources by surviving, non-target species (Stahlheber

et al. 2015). How rapidly these changes accrue, how long they persist after woody plants are removed, and whether they impede grassland reassembly, are not well understood (Stahlheber et al. 2015). We explore these questions by comparing rates of community reassembly following tree removal from experimental plots comprising a fine-scale mosaic of encroachment states: remnant meadow openings and areas of recent invasion (minimally altered by trees) to century-old forests (largely lacking in meadow species; Halpern et al. 2010). Two elements of our design permit strong inferences about the role of past tree influence and the success of restoration: a detailed, spatially explicit understanding of encroachment history and its effects on meadow community structure (Haugo and Halpern 2007), and the proximity of high-quality reference sites, often lacking in restoration studies (Thorpe and Stanley 2011).

Ecological restoration seeks to reestablish not only the species' assemblages, but the ecological processes that historically defined a system (SER 2004). However, reintroducing disturbance processes, such as fire, into systems that are highly altered or degraded may be impractical, ineffective, or counterproductive (Briggs et al. 2005, Hobbs et al. 2006, MacDougall et al. 2013). For example, when fuel levels are uncharacteristically high, prescribed burning can have adverse effects on native vegetation and soils (Haskins and Gehring 2004, Creech et al. 2012), allowing undesirable species to establish (D'Antonio and Vitousek 1992, D'Antonio 2000, Keeley 2006, Stanley et al. 2011). Surrogate treatments (e.g., mowing or herbicide) may be as effective as fire if they alter resource conditions to favor the establishment or growth of desired species (MacDougall and Turkington 2007, but see Scholtz et al. 2018). In this study, we explore whether disturbance by fire, assumed to be integral to most grasslands, thus critical for restoration, enhances or impedes reassembly once trees are removed, or whether effects of fire depend on past tree influence.

The effectiveness of restoration may also hinge on the specificity of the metrics used to gauge success. For example, Brudvig et al. (2017) have proposed a “hierarchy of predictability” that ranks community metrics along a continuum, from those based on structural attributes (high predictability of outcomes) to those based on taxonomic composition (low predictability). This continuum reflects the theoretical expectation that community assembly should be deterministic (predictable) with respect to the functional traits of species, but “historically contingent” (unpredictable) with respect to species' identities (Wilson 1999, Temperton et al. 2004, Fukami et al. 2005, Li and Shipley 2018). Functional-trait assembly is driven by non-neutral or niche-based processes (e.g., environmental filtering or resource partitioning) that favor particular sets of physiological, morphological, or life-history traits (Fargione et al. 2003, Kraft et al. 2008, Petermann et al. 2010). Because species' pools typically contain taxa with similar traits (e.g., growth forms), multiple patterns of species'

establishment can yield similar outcomes. In contrast, taxonomic or species assembly is susceptible to stochastic effects, notably, the chance arrival of species and resulting priority effects (Fox 1987, Belyea and Lancaster 1999, Walker and del Moral 2003). Here, we test the hypothesis that community reassembly will yield greater similarity to the physical structure (abundance and diversity of plant growth forms) than to the species composition of uninvaded grasslands (Fig. 1a). This test is motivated not only by theory, but by practical considerations. Recent debates address the merits and limitations of trait-based vs. taxonomic metrics of restoration success (Durigan and Sukanuma 2015, Reid 2015, Sukanuma and Durigan 2015, Brancalion and Holl 2016). Although restoration of species composition is desirable, it may not be possible if target species have been lost and recolonization is dispersal- or establishment-limited (Dzwonko and Loster 1998, Muller et al. 1998, Bakker and Berendse 1999, Damschen et al. 2008, Helsen et al. 2013). However, restoration of community structure (e.g., growth-form abundance and diversity) and associated functions (e.g., provision of floral resources, forage, or habitat), may be possible if surviving or more vagile species of similar form or function show compensatory responses (a form of species redundancy; Walker 1992, Tilman and Downing 1994, Naem 1998).

Whether reassembly is gauged by trait-based or taxonomic metrics, temporal changes in structure or species composition can be described by two general properties: progression of treated sites toward the reference state (Fig. 1a), and the degree to which treated sites converge or diverge, independent of the reference state (Fig. 1b; Matthews and Spyreas 2010). When target species have been lost from a system, progression toward the reference state may be constrained by seed limitation (Foster and Tilman 2003, Ozinga et al. 2005, Helsen et al. 2013, Grman et al. 2015) or by factors that inhibit establishment (Young et al. 2001, Martin and Wilsey 2012, Fukami 2015, Kraft et al. 2015). Convergence or divergence of reassembling communities may depend on their similarity prior to intervention; whether disturbance enhances or reduces environmental heterogeneity, promoting divergence or convergence, respectively; chance colonization events that lead to priority effects and divergence; or establishment of invasive species, forcing convergence (Trowbridge 2007, Aronson and Galatowitsch 2008, Matthews and Spyreas 2010).

Here, we explore how both properties of grassland community reassembly—progression toward the reference state (Fig. 1a) and convergence or divergence independent of the reference state (Fig. 1b)—could be mediated by past tree influence or fire. We hypothesized that, following tree removal, progression of treated sites toward the reference state would be more predictable in structural than in compositional terms ( $H_1$ , Fig. 1a). We hypothesized several possible (alternative) responses to fire. Specifically, we hypothesized that fire could promote reassembly ( $H_2$ , e.g., by reducing competition from

residual forest herbs or by enhancing light or soil resources); that fire could inhibit reassembly ( $H_3$ , e.g., by reducing survival and local sources of seed of desired species); or that effects of fire could vary with past tree influence ( $H_4$ , e.g., via a shift in the mechanisms regulating reassembly). Given the heterogeneity of past tree influence, we hypothesized that colonization by meadow species would promote convergence of composition and structure ( $H_5$ ), with fire either reinforcing ( $H_6$ ) or tempering this effect ( $H_7$ ), depending on its severity or variability.

## STUDY AREA

Bunchgrass Ridge forms a gently sloping plateau at 1,350 m elevation in the Willamette National Forest, Oregon (USA). It is on the western edge of the High Cascades Province, between the geologically older western Cascades (volcanic flows and pyroclastic deposits of Oligocene and Miocene origin) and the younger High Cascade peaks (Quaternary shield and composite volcanoes; Orr et al. 1992).

The climate of the region is maritime, with cool, wet winters and warm, dry summers. Climate data from the nearest weather station at a comparable elevation (Santiam Pass, 1,488 m) are illustrative. Average minimum and maximum temperatures are  $-6.6^{\circ}\text{C}$  and  $-0.2^{\circ}\text{C}$  in December and  $6.5^{\circ}\text{C}$  and  $22.1^{\circ}\text{C}$  in August. Annual precipitation averages  $\sim 2,290$  mm, but is highly seasonal, with 14% falling from June through September (data record for 1981–2010; Western Regional Climate Center; data *available online*).<sup>6</sup> Thus, despite high annual precipitation, summer drought is common. Annual snowfall can exceed 11 m and a snowpack can persist into May or early June (data record for 1948–1985; Western Regional Climate Center; data *available online*).<sup>7</sup>

The 100-ha study site supports a mosaic of open meadows (or grasslands) and patches of forest of varying age, reflecting two centuries of conifer encroachment (Fig. 2). Open areas are dominated by graminoids, forbs, and shrubs characteristic of mesic- and dry-site meadows of the region (McCain et al. 2014). Once trees establish, however, meadow species are gradually replaced by shade-tolerant forest herbs (Haugo and Halpern 2007). The strong dependence of meadow species composition on forest age structure permits use of current species composition (or other community metrics) as proxies for past tree influence (Halpern et al. 2016; Appendix S1: Table S1).

The topography of the study area is gentle (slopes  $<5\%$ ) and soils are homogeneous. Soil profiles suggest dominance of grassland vegetation for centuries, if not millennia, prior to recent encroachment (D. Lammers, *personal communication*). Soils are deep, fine to very fine

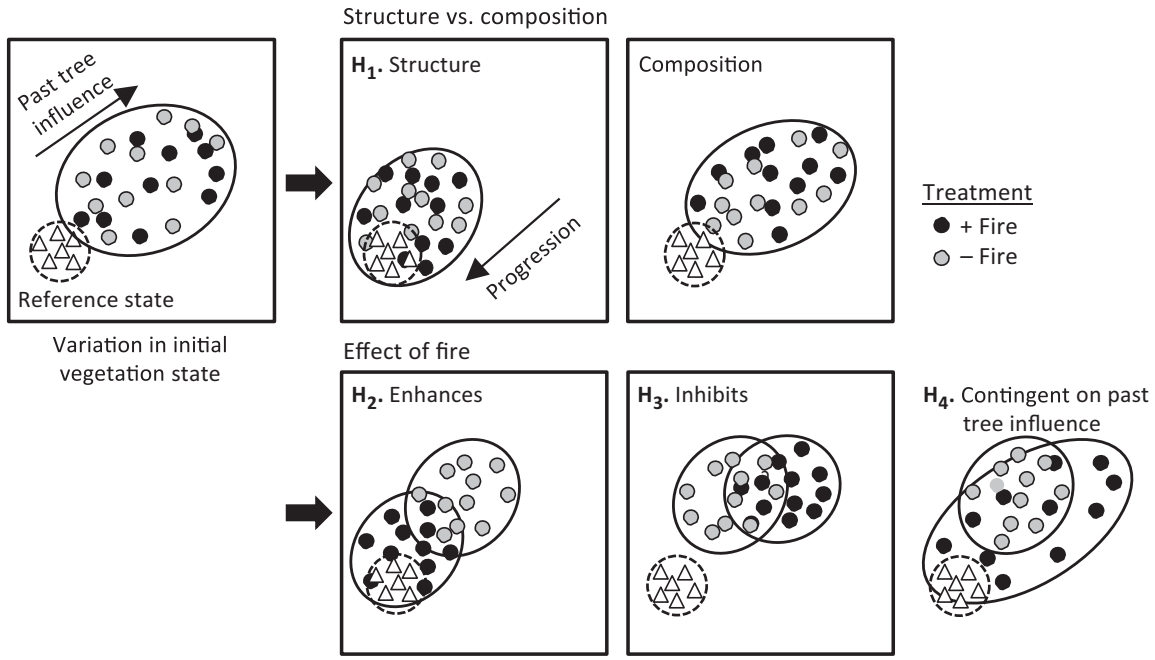
<sup>6</sup> <https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?or7559>

<sup>7</sup> <https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?orsant>

sandy loams, derived from andesitic basalt and tephra with varying amounts of glacial rock. They grade from Vitric Melanocryands in open meadows to Aquic

Vitricryands in areas of older encroachment. Soil biogeochemical properties are described by Griffiths et al. (2005).

**a. Progression toward reference state**



**b. Convergence vs. divergence of treated sites**

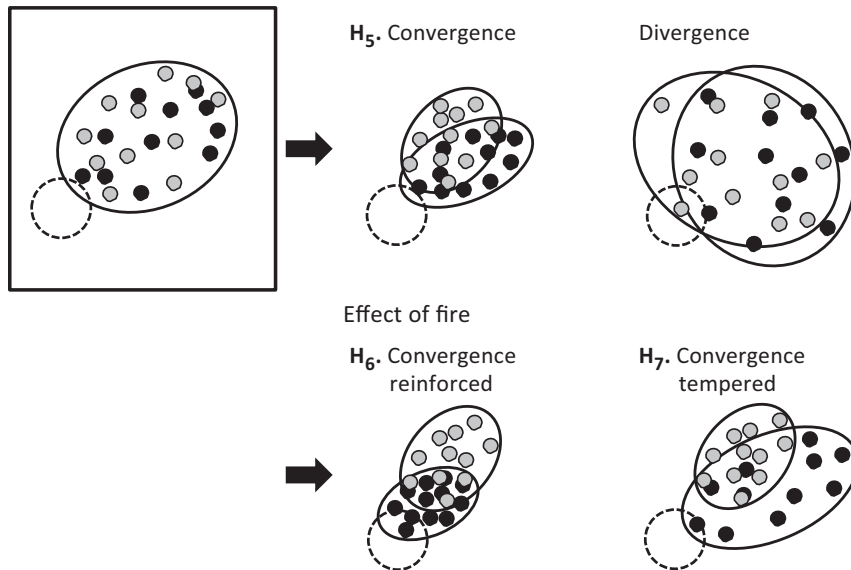


FIG. 1. Properties and alternative outcomes of grassland community reassembly after tree removal, with or without fire, from a range of initial vegetation states (proxy for past tree influence). (a) Progression of treated sites toward the reference state: reassembly should result in greater similarity to reference-state structure than to reference-state composition ( $H_1$ ). Fire can enhance ( $H_2$ ) or inhibit ( $H_3$ ) reassembly, or its effects can vary with past tree influence ( $H_4$ ). (b) Convergence vs. divergence of treated sites, independent of the reference state: reestablishment of grassland species should reduce initial heterogeneity, leading to convergence ( $H_5$ ). Convergence can be reinforced ( $H_6$ ) or tempered ( $H_7$ ) by fire, depending on its severity or heterogeneity.



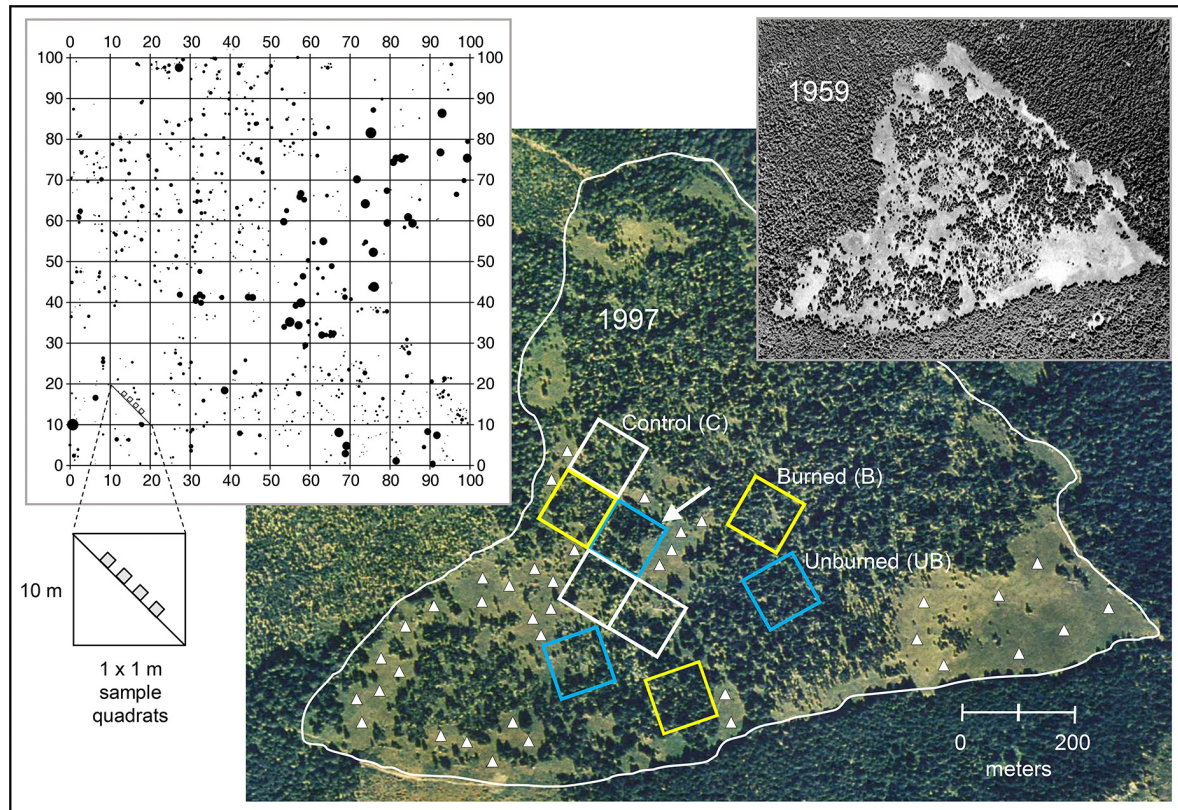


FIG. 2. Historical aerial photos of the study area showing the locations of the 1-ha (100 × 100 m) experimental plots (colored by treatment) and reference meadows. The solid white outline is the extent of former meadow (prior to 19th-century encroachment). Triangles represent multiple reference meadow transects. Trees visible in the 1959 photo had established in the 19th century, but most infilling of meadows occurred in the second half of the 20th century. The 1-ha stem map corresponds to the plot marked by the white arrow and illustrates the fine-scale mosaic of encroachment states. All trees  $\geq 1.4$  m tall were aged; symbol size corresponds to age. Within each plot, 32 or 64 of the 10 × 10 m subplots were sampled for vegetation using four 1 × 1 m quadrats spaced along a diagonal transect. The same quadrat-based design was used for reference meadow transects.

Although the causes of recent encroachment remain unclear, the patterns are well documented. The principal invaders, *Abies grandis* and *Pinus contorta*, established together during two distinct periods: the late 19th century (sparse invasion) and the second half of the 20th century (extensive invasion; Halpern et al. 2010, Rice et al. 2012), reducing the area of open meadow by  $>50\%$  (Rice 2009). Although one or more factors may have triggered periods of invasion, none can explain the recent pattern of sustained recruitment over multiple decades. Establishment dates are only weakly correlated with spring snowpack, summer precipitation, and temperature (Halpern et al. 2010, Rice et al. 2012). Moreover, *Abies* establishment increased under conditions that typically inhibit germination and survival (warmer, drier summers), then declined under conditions more conducive to both (cooler, wetter summers; Rochefort et al. 1994, Miller and Halpern 1998). Although recent invasion may be linked to cessation of sheep grazing, common in the Cascades in the early 1900s (Elliot 1946, Johnson 1985), there is no documented history of

grazing at Bunchgrass Ridge. Similarly, recent invasion could reflect a reduction in fire frequency, but there is no evidence of such a change. At this elevation, natural ignitions are infrequent ( $>100$  yr; Morrison and Swanson 1990, Weisberg and Swanson 2003, Tepley et al. 2013) and, although anthropogenic burning of meadows occurred historically in this region (Burke 1979, Boyd 1999), there is no evidence of fire of sufficient severity to have scarred trees in or adjacent to the plots. On the other hand, there is strong evidence from dendrochronological and spatial point pattern analyses that, once trees established, positive feedbacks promoted rapid conversion to forest (Halpern et al. 2010, Rice et al. 2012). Designated as a Special Habitat Area, Bunchgrass Ridge was identified as a priority area for restoration in the 1990 Forest Plan for the Willamette National Forest. The current experiment, developed with natural resource managers on the Forest, was designed to test the efficacy and operational feasibility of alternative restoration approaches, including tree removal and prescribed fire.

## METHODS

*Site selection and experimental design*

Following extensive field reconnaissance in 2002, we delineated a 16-ha area of tree-invaded meadows for experimentation (Fig. 2). In 2003, we established nine,  $100 \times 100$  m (1-ha) plots, each encompassing a fine-scale mosaic of encroachment states, including residual meadow openings and areas of recent (20th-century) or older (19th-century) encroachment (Fig. 2). Four of these plots were used to reconstruct the invasion history and associated changes in vegetation (Haugo and Halpern 2007, Halpern et al. 2010). All plots were randomly assigned to one of three treatments: control (C, no trees removed), unburned (UB, all trees removed and woody residues hand-piled and burned, leaving 90% of the ground surface unburned), or burned (B, all trees removed and woody residues broadcast burned; Fig. 2). Here we consider only UB and B plots.

Trees were felled in January and February 2006 on deep, compacted snow to minimize soil disturbance. Skidders were used to yard tree boles to an off-site landing; limbs were left attached to reduce fuel accumulation. In UB plots, slash piles were constructed in June 2006 away from vegetation transects (see *Sampling methods*). Piles were ignited in November 2006 and burned to completion (95–100% consumption) within two days (Halpern et al. 2014). In B plots, fine (1- to 100-h) fuel loads averaged 53–69 Mg/ha. Fires were ignited in September 2006 and burned to completion within 2 h; flame lengths were 1–2 m and fine fuel consumption averaged 67–87% among plots.

*Sampling methods*

Within each experimental plot, we established a permanent grid of 100,  $10 \times 10$  m subplots (sampling units; Fig. 2). Subplots on the perimeter of each plot were treated as experimental buffers and excluded from sampling. We sampled all (64) or half (32) of the non-perimeter subplots (160 per treatment) to capture the full range of encroachment (initial vegetation) states (Haugo and Halpern 2007). Within each subplot, we visually estimated the canopy cover of each vascular plant species (maximum of 100%) in each of four  $1 \times 1$  m quadrats evenly spaced along a diagonal transect (Fig. 2). In the burned (B) treatment, we also estimated burn severity in each quadrat as total cover of white ash, blackened duff, and charcoal (maximum of 100%). We sampled prior to tree removal (2004) and resampled in 2007, 2009, and 2013 (2, 4, and 8 yr after tree removal; 1, 3, and 7 yr after burning).

In 2013, we also sampled adjacent uninvaded meadows, reference sites representing a diversity of meadow types, including both forb-rich and less diverse communities dominated by perennial bunchgrasses (*Festuca idahoensis* or *Achnatherum occidentale*) or the subshrub,

*Phlox diffusa*. Reference meadows (RM) were contiguous with or adjacent to the experimental plots and had comparable topography and soils (Fig. 2). In total, we sampled 117 RM transects, using the same number, size, and spacing of quadrats as in the experimental subplots (Fig. 2). Transects had a haphazard start and random azimuth, but were constrained to avoid forest edges. Although sampling was limited to 2013, we assumed that any temporal variation in RM composition was small relative to the post-disturbance changes in the experimental subplots (Halpern et al. 2012). A previous assessment of annual turnover supports this assumption: among 210,  $1 \times 1$  m, meadow quadrats sampled in consecutive years, only 1% and 3% of species' records represented loss or colonization events, respectively (C. B. Halpern, *unpublished data*). Nomenclature follows USDA Plants (*available online*).<sup>8</sup>

*Data reduction*

We analyzed reassembly as multivariate responses in both species and structural space. Given the focus on meadow community reassembly, we limited our analyses to species that are characteristic of uninvaded reference sites (Appendix S1: Table S2). Forest species were dropped from the analyses for two reasons. First, although they varied in abundance prior to tree removal (contingent on past tree influence; Appendix S1: Table S1), they contributed minimally afterward (80–90% declines in cover; Halpern et al. 2012, 2016). Second, by removing them from the analyses, our interpretation focuses on the post-treatment colonization and growth of meadow species, not on the pre-treatment variation and differential loss of forest species. Ruderal species, which were uncommon before and after treatment, were also dropped (Halpern et al. 2012). Prior to analyses, species cover and burn severity values were averaged among quadrats within each subplot.

Community structure was characterized by the cover and diversity of the principal plant growth forms: sedges, grasses, forbs, and subshrubs. These groups play distinct functional roles in grasslands (Fargione et al. 2003), reflecting variation in their morphological traits (leaf and stem form, location of perennating buds, or clonality) and related ecosystem services (floral resources for pollinators, forage or seeds for wildlife, or habitat structure). Each subplot was characterized by six structural variables: summed cover of species of each growth form and richness of grass and forb species. We did not consider richness of sedges or subshrubs because their species' pools were very small (Appendix S1: Table S2).

*Analyses*

We used parallel analytical approaches to compare changes in the composition and structure of

<sup>8</sup> <https://plants.usda.gov>

experimental subplots in response to tree removal, fire, and past tree influence ( $H_1$ , Fig. 1). Ordination was used to graphically portray the changing relationships of experimental subplots to reference meadows. Nonmetric multi-dimensional scaling (NMS; Kruskal 1964) was used for compositional data and principal components analysis (PCA) for structural data. Both sample matrices included RM transects ( $n = 117$ ) and the full set of experimental subplots (UB and B) at each sampling date ( $n = 1280$ ), less 11 samples containing no meadow species (10 pre-treatment, one post-treatment). For the NMS (composition), uncommon species (present in <1% of samples) were dropped and cover was arcsine square-root transformed. We used Bray-Curtis as the distance measure, a random starting configuration, a maximum of 500 iterations (250 runs with real and randomized data), and an instability criterion of 0.0000001 (McCune and Grace 2002). We applied a Varimax rotation to the final three-dimensional solution (stress of 14.5) to maximize the distribution of samples along the axes. For the PCA (structure), cover and richness were log- and square-root transformed, respectively, then standardized (zero mean, unit variance). NMS and PCA were run in PC-ORD ver. 6.0 (McCune and Mefford 2011).

*Progression toward reference meadow.*—We used two approaches to assess the progression (reassembly) of experimental subplots toward RM as influenced by fire ( $H_2$  and  $H_3$ ). First, we used convex hulls to define the bounds of RM transects in three-dimensional compositional or structural space. We then characterized the progression to RM as a binary condition: subplot presence inside or outside of the RM hull. Convex hulls were generated in R version 3.1.2 using the *geometry* package version 0.3-6 (Barber et al. 2015). Subplot presence within the hull was determined with the *ptmpoly* package version 2.4 (Maisog et al. 2014). We used chi-square ( $\chi^2$ ) tests to determine, at each sampling date, whether treatments (UB vs. B) differed in the proportion of subplots moving into or out of the RM hull relative to initial positions. The 11 samples excluded from the ordinations due to lack of meadow species were defined as outside the hull.

The second approach treated the progression of experimental subplots as a continuous measure of dissimilarity or distance from RM. For each sampling date, we computed the mean Bray-Curtis (compositional) dissimilarity or Euclidean (structural) distance between each subplot and all RM transects ( $n = 117$ ). We used these distances to make three types of comparisons among treatments. First, we used  $\chi^2$  tests to determine whether the proportion of subplots that declined in distance to RM between initial (2004) and final (2013) sampling differed between treatments. Second, we used frequency histograms for each treatment to illustrate the changing distributions of distance over time between subplots and RM transects ( $n = 155$ – $160$  plots and thus distances per treatment). Kolmogorov-Smirnov (KS)

tests were used to determine whether these distributions changed between initial and final sampling within each treatment and whether they differed between treatments at each sampling date. Finally, we used linear mixed models to test whether the mean distance to RM (average of subplots within plots) declined with time and whether the magnitude of decline differed between treatments. Fixed effects included time (categorical), burn treatment (UB vs. B), and their interaction; plot was treated as a random effect to account for its repeated measurement.

We also used linear mixed models to test whether compositional and structural responses to fire were contingent on past tree influence ( $H_4$ ), using subplot distance to RM at final sampling as the response variable. Fixed effects included initial distance to RM, burn treatment (UB vs. B), and their interaction; plot was treated as a random effect to account for the nesting of subplots within plots. For plots in the burned (B) treatment we also tested the influence of burn severity, modeling final distance to RM as a function of initial distance, burn severity (total cover of white ash, blackened duff, and charcoal) and their interaction (fixed effects); plot was treated as a random effect.

Linear mixed models were run using the *lme4* package (Bates et al. 2015) in R version 3.4.3 (R Core Team 2017).  $P$  values were computed using Satterthwaite's degrees of freedom method in the *lmerTest* package (Kuznetsova et al. 2017). We used marginal  $R^2$  (Nakagawa and Schielzeth 2013) as a measure of the variation explained by the fixed effects in each model.

To aid with the interpretation of treatment effects, we conducted an indicator species analysis (Duf rene and Legendre 1997). Burn treatment (UB or B) or reference meadow (RM) were used as the grouping variable with data limited to the 2013 measurement. Of 43 taxa, 30 were frequent enough to test (Appendix S1: Table S2). A species was considered a treatment or RM indicator only if its maximum indicator value ( $IV_{\max}$ ) was both significant ( $P \leq 0.05$ ) and exceeded 25 (Duf rene and Legendre 1997). We chose this threshold because with large sample sizes, randomization tests can produce statistically significant results for indicator values that are small (i.e., less meaningful, ecologically). The analysis was conducted in PC-ORD ver. 6.0 (McCune and Mefford 2011).

*Compositional and structural convergence among subplots.*—We tested whether experimental subplots converged (or diverged) in composition or structure, independent of their progression toward RM ( $H_5$ ), and whether any trend was reinforced ( $H_6$ ) or tempered by fire ( $H_7$ ). We defined convergence within a treatment as a significant decline in the average Bray-Curtis dissimilarity or Euclidean distance among subplots within plots (i.e., a decline in heterogeneity within plots). We used linear mixed models to test whether heterogeneity declined between initial and final sampling and whether



the magnitude of decline differed between treatments. Fixed effects included time (categorical), burn treatment (UB vs. B), and their interaction; plot was treated as a random effect to account for the repeated measurement. Post-hoc comparisons of means were used to interpret significant interactions, focusing on contrasts between initial and final values (within or between treatments). Models were run using the *lme4* package (Bates et al. 2015) in R version 3.4.3 (R Core Team 2017). *P* values were computed using Satterthwaite's degrees of freedom method in the *lmerTest* package (Kuznetsova et al. 2017). Marginal  $R^2$  (Nakagawa and Schielzeth 2013) was used as a measure of the variation explained by the fixed effects in each model.

## RESULTS

### *Initial variation in composition and structure*

Prior to tree removal (2004), experimental subplots varied widely in their composition and structure (Figs. 3, 4), reflecting the mosaic of encroachment states (residual meadow openings to >140-yr-old forests). Among subplots, total (summed) cover of meadow species ranged from 0% to 140% and richness from 0 to 17 species. In contrast, reference meadows occupied distinct regions of compositional and structural space, despite some overlap with experimental subplots. Reference meadows (RM) were characterized by greater cover and richness of grasses and forbs (negative correlations with PCA1) and greater cover of subshrubs (negative correlation with PCA2; Fig. 4, Table 1). Among RM transects, total cover of meadow species ranged from 37% to 136% and richness from 5 to 21 species (for growth-form totals, see Appendix S1: Table S2).

### *Progression toward reference meadow*

*Movement into or out of the reference meadow hull.*—Prior to tree removal, most experimental subplots lay outside the hulls defining RM composition and structure (Figs. 3, 4). In total, 92.8% lay outside the compositional hull and 85.6% lay outside the structural hull. Movement of subplots relative to the compositional and structural hulls was consistent with  $H_1$  (greater reassembly of structure than of composition). Of 274 subplots initially outside the hulls, 31 (11.3%) moved into the structural hull, but none entered and remained in the compositional hull (Table 2). Moreover, of subplots initially within the hull, a greater percentage moved out for composition (73.9%, 17 of 23) than for structure (60.9%, 28 of 46; Table 2).

Fire did not affect subplot movement out of the compositional or structural hull, but it did inhibit movement into the structural hull, consistent with  $H_3$ . Specifically, movement out of the hull did not differ between UB and B for either composition (100% vs. 68.4%;  $\chi^2 = 0.46$ ,  $P = 0.50$ ) or structure (53.3% vs. 75.0%;  $\chi^2 = 1.25$ ,

$P = 0.26$ ; Table 2). However, for structure, a significantly greater percentage of UB subplots entered the RM hull than did B subplots (15.3% vs. 6.9%, respectively;  $\chi^2 = 3.96$ ,  $P = 0.047$ ; Table 2).

The net result of subplot movement into and out of the RM hulls was also consistent with  $H_1$  (greater reassembly of structure than of composition) and  $H_3$  (reassembly inhibited by fire). Over the study period, subplot presence in the structural hull increased by 62.5% in UB but decreased by 23.3% in B (Table 2). In contrast, both treatments showed a net loss of subplots from the compositional hull (100% of UB, 68.4% of B).

*Changes in distance to reference meadows.*—Tree removal enhanced the progression toward RM in a vast majority of subplots, but fire tempered this effect, consistent with  $H_3$ . Specifically, distance to RM declined from initial (2004) to final (2013) sampling for a smaller percentage of B than of UB subplots for both composition (63.2% vs. 86.5%;  $\chi^2 = 21.17$ ,  $P < 0.0001$ ) and structure (70.3% vs. 87.1%;  $\chi^2 = 13.01$ ,  $P = 0.0003$ ). The effect was most apparent one year after burning (2007) when distance to RM increased in many B but not UB subplots (Figs. 3, 4). Over time, however, distributions of distance narrowed in both treatments, with final distributions differing significantly from initial distributions ( $P < 0.0001$  for KS tests within treatments). At final sampling, distributions of compositional distance did not differ statistically between treatments ( $P = 0.27$ ; Fig. 3) but distributions of structural distance did ( $P = 0.0009$ ; Fig. 4). The difference for structure reflected the greater number of more distant subplots in B, subplots with distinctly greater cover of sedge and lower cover and richness of forbs and grasses (2013 panel, Fig. 4). Despite the narrowing of distributions over time, at final sampling the vast majority of subplots in both treatments remained more distant from RM than the average distance among RM transects themselves (Figs. 3, 4). At final sampling, average cover of bare ground remained higher in UB (11%) and B (17%) than in RM (6.5%), and total cover of meadow species remained lower (49% and 52%, respectively) than in RM (79%).

Temporal trends in mean (plot-scale) distance to RM did not support  $H_2$  (fire promotes reassembly) or  $H_3$  (fire inhibits reassembly). Although we detected significant declines in compositional and structural distance at final sampling (2013), any difference between treatments in the magnitude of decline did not persist beyond 2007 (Appendix S1: Table S3).

*Indicator species.*—Of 30 meadow species tested, 12 were significant indicators of RM (Table 3). Although few RM indicators responded negatively to tree removal alone (UB), many responded negatively to burning (B) (Appendix S1: Table S2). Those most sensitive to fire included the bunchgrass, *Festuca idahoensis* (47% reduction in frequency, 85% reduction in cover), and forbs in the Asteraceae family: *Achillea millefolium*, *Agoseris*



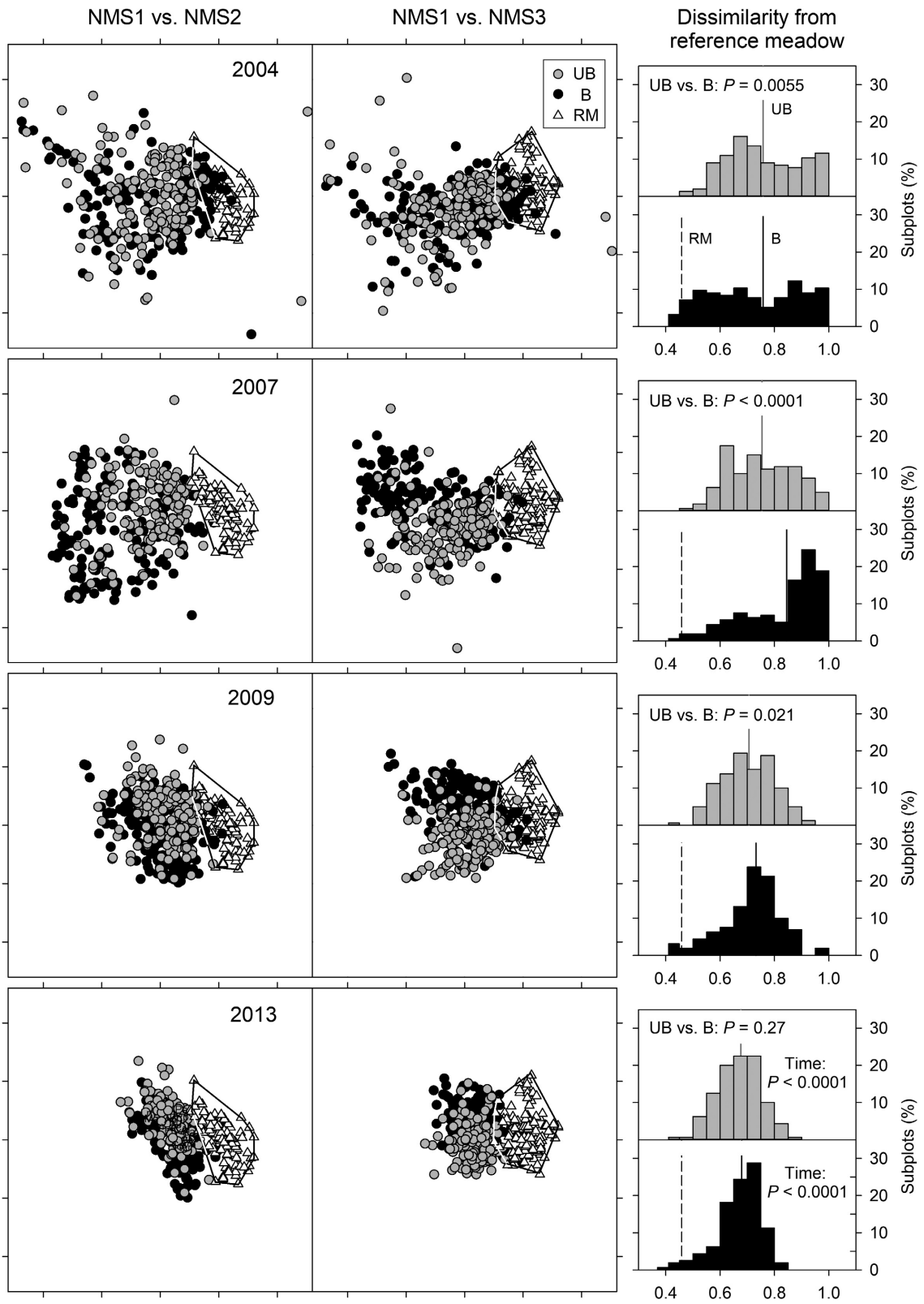


FIG. 3. Nonmetric multi-dimensional scaling ordination of unburned (UB) and burned (B) subplots illustrating temporal changes in species composition relative to reference meadow (RM) transects (circumscribed by a convex hull). For clarity, separate panels show subplot positions at each sampling date (left and center columns are different pairs of ordination axes). Histograms summarize frequency distributions of subplot distances (Bray-Curtis dissimilarity) from RM transects. Solid vertical lines are treatment means ( $n = 3$  plots); the dashed vertical line is the mean distance among RM transects ( $n = 117$ ).  $P$  values are from Kolmogorov-Smirnov tests of frequency distributions comparing treatments within years (UB vs. B) or between initial and final sampling within treatments (Time, 2013 panels). See Appendix S1: Table S3a for linear mixed-model results of mean (plot-scale) compositional distances to RM.

*aurantiaca*, *Erigeron aliciae*, and *Hieracium scouleri* (19–65% reductions in frequency, 65–80% reductions in cover).

Six meadow species were significant indicators of the experimental treatments (Table 3). Three were indicators

of UB: the grasses, *Elymus glaucus* and *Bromus carinatus* (2–4 × the cover as in RM), and the stoloniferous forb, *Fragaria* spp. (2× as frequent and 8× the cover as in RM). Three were indicators of B: the sedge, *Carex inops* spp. ( $2\times$  the cover as RM); and the forbs, *Cirsium*

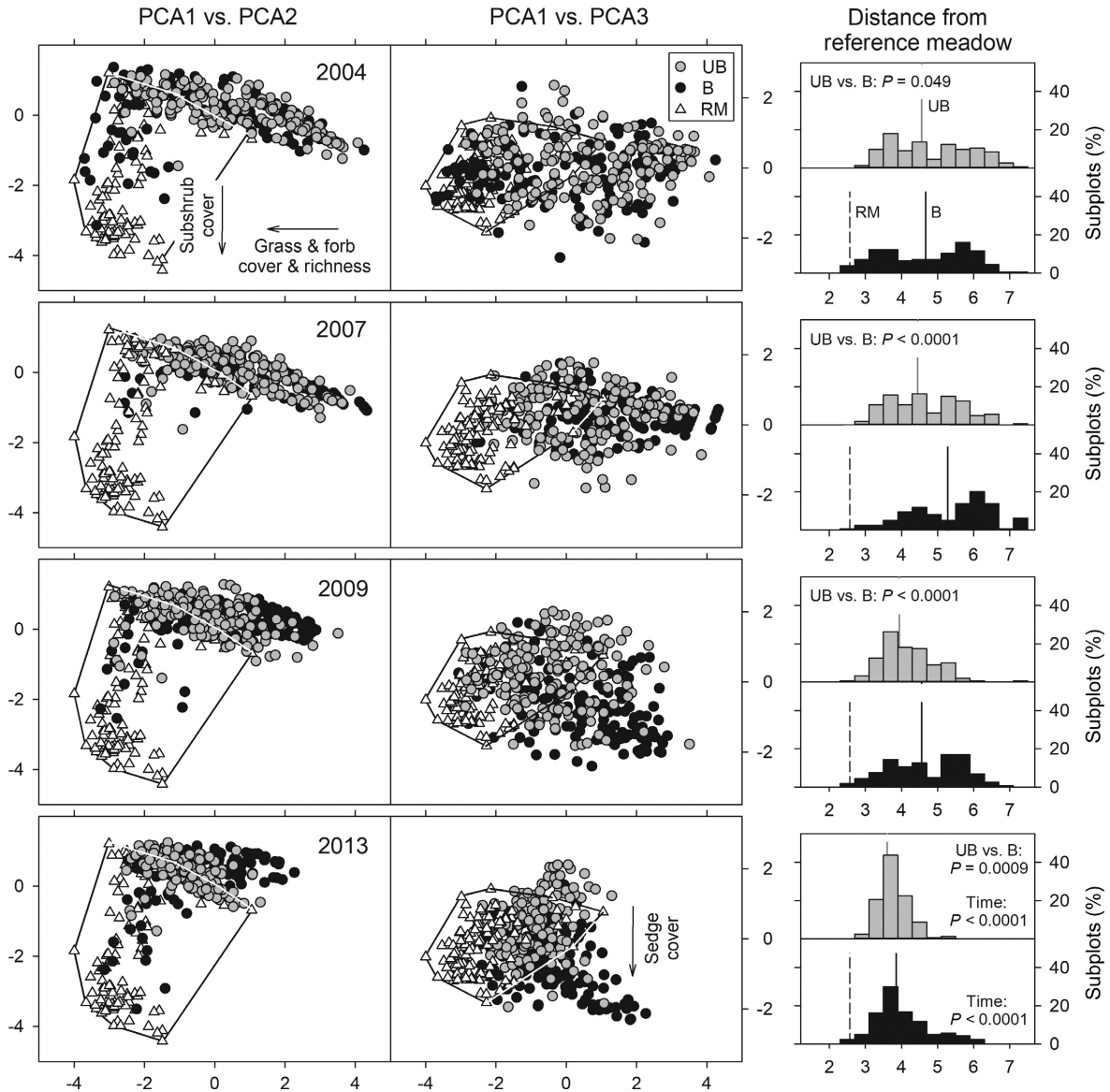


FIG. 4. Principal components analysis ordination of unburned (UB) and burned (B) subplots illustrating temporal changes in community structure relative to reference meadow (RM) transects (circumscribed by a convex hull). See Appendix S1: Table S3b for linear mixed-model results of mean (plot-scale) structural distances to RM. See Fig. 3 for other details.

TABLE 1. Results of principal components analysis of meadow community structure for subplots representing the two experimental treatments and reference meadows (see Fig. 4).

Axis	Eigen-value	Percentage of variance	Cumulative percentage of variance	Growth-form correlations with axes					
				Grass cover	Forb cover	Grass richness	Forb richness	Subshrub cover	Sedge cover
1	3.29	54.8	54.8	<b>-0.82</b>	<b>-0.82</b>	<b>-0.87</b>	<b>-0.81</b>	-0.48	-0.55
2	0.86	14.3	69.1	-0.01	0.24	-0.08	0.12	<b>-0.82</b>	0.33
3	0.78	12.9	82.0	0.34	0.10	0.22	-0.29	-0.29	<b>-0.72</b>
4	0.65	10.9	92.9						
5	0.25	4.2	97.2						
6	0.17	2.8	100.0						

Note: Growth-form correlations with axes are limited to the first three axes; boldface type denotes a correlation  $>|0.7|$ .

*remotifolium* (3× the cover as in RM) and *Vicia americana* (4× as frequent and 11× the cover as in RM; Appendix S1: Table S2).

*Effects of past tree influence and its interaction with fire.*—For both composition and structure, final distance from RM was positively related to initial distance (past tree influence; Fig. 5; Appendix S1: Table S3). However, the relative progression to RM varied with initial distance (regression slopes  $<1$ , Fig. 5). Among subplots with limited tree influence (smaller initial distances), final distances were as or more likely to increase as to decrease, particularly with fire. However, for subplots initially more distant from RM (greater tree influence), final distances typically decreased (see histograms, Fig. 5). Burning affected the slope of the relationship for structure, consistent with  $H_4$  (fire effects vary with past tree influence), reducing the progression to RM to a greater degree in subplots with greater tree influence (significant treatment  $\times$  initial distance interaction; Fig. 5b; Appendix S1: Table S4a). Burning did not have a similar effect on composition (Fig. 5a; Appendix S1: Table S4a).

Within the burned (B) treatment, burn severity varied widely (range of 0–99%; median of 71%). For composition, final distance to RM was positively related to initial distance and burn severity, and negatively related to their interaction (Appendix S1: Table S4b), indicating that effects of severity were stronger in subplots initially more similar to RM. Burn severity did not have a similar effect on structural reassembly (Appendix S1: Table S4b).

#### *Compositional and structural convergence within plots*

Compositional heterogeneity within plots declined between initial and final sampling, irrespective of burn treatment, consistent with  $H_5$  (convergence of subplots during reassembly; Fig. 6a; Appendix S1: Table S5). In contrast, structural heterogeneity declined only in the absence of fire (significant time  $\times$  treatment interaction; Fig. 6b; Appendix S1: Table S5), consistent with  $H_7$  (tempering of convergence by fire).

## DISCUSSION

In this experiment, we tested whether, and under what conditions, tree removal, with or without fire, can promote natural reassembly of mountain grasslands, reversing the effects of a regime shift to forest. We asked whether conclusions about treatment effectiveness hinge on the community attribute (composition or structure) used to gauge success. Using initial vegetation state as a proxy for past tree influence, we asked whether community reassembly is sensitive to the degree of alteration by trees, one of few restoration studies to explicitly address this question. We also tested whether fire, assumed to maintain the open nature of grasslands, enhances or impedes reassembly, or varies in its effects depending on past tree influence. Eight years after treatment, our results confirm early observations: tree removal, with or without fire, effectively shifted dominance from shade-tolerant forest herbs to native meadow forbs and graminoids (Halpern et al. 2012), while triggering only limited reinvasion by conifers (Kremer et al. 2014). However, comparisons to uninvaded reference sites indicate only partial reassembly of meadow composition and structure, highlighting the strong legacies of past tree influence and adverse effects of fire.

#### *Reassembly of composition vs. structure*

We tested the theoretical expectation ( $H_1$ ) that community reassembly would lead to greater predictability of structure than of composition (Fukami et al. 2005, Helsen et al. 2012, Brudvig et al. 2017, Laughlin et al. 2017, Li and Shipley 2018). Our results were largely consistent with this expectation. Structural distance to reference meadow declined for a greater proportion of subplots than did compositional distance. Moreover, a greater proportion of subplots entered, and fewer departed from, the reference meadow structural hull than the compositional hull. The net effect of these changes was a small gain (6.5%) in subplot presence in the structural hull, but a major loss (74%) from the compositional hull. This contrast underscores two important results: not only was compositional reassembly rare, but

TABLE 2. Experimental subplot locations, relative to the reference meadow compositional and structural hull, at initial and final sampling, and results of chi-square ( $\chi^2$ ) tests comparing subplot movement into and out of the hull.

Location (initial or final) or direction of movement	Composition				$\chi^2$	<i>P</i>	Structure				$\chi^2$	<i>P</i>
	Unburned (UB)		Burned (B)				Unburned (UB)		Burned (B)			
	<i>n</i>	%	<i>n</i>	%			<i>n</i>	%	<i>n</i>	%		
2004												
Initial, outside the hull	156	97.5	141	88.1			144	90.0	130	81.3		
Initial, inside the hull	4	2.5	19	11.9			16	10.0	30	18.7		
2007												
Movement into the hull	0	0.0	0	0.0	—	—	12	8.3	4	3.1	2.54	0.11
Movement out of the hull	4	100.0	15	78.9	0.08	0.78	8	50.0	18	60.0	0.12	0.73
2009												
Movement into the hull	1	0.6	1	0.7	—	—	8	5.6	12	9.2	0.86	0.35
Movement out of the hull	1	25.0	11	57.9	0.42	0.52	12	75.0	17	56.7	0.82	0.36
2013												
Movement into the hull	0	0.0	0	0.0	—	—	22	15.3	9	6.9	3.96	<b>0.047</b>
Movement out of the hull	4	100.0	13	68.4	0.46	0.50	12	75.0	16	53.3	1.25	0.26
2013												
Final, outside the hull	160	100.0	154	96.2			134	83.7	137	85.6		
Final, inside the hull	0	0.0	6	3.8			26	16.3	23	14.4		

Notes: The variable *n* is the number of subplots (out of 160). A significant ( $P \leq 0.05$ ) difference between treatments is indicated by boldface type. Subplot movement into or out of the hull is based on the initial location (2004). Dashes indicate that sample sizes were too small to test.

where past tree influence was limited (i.e., in residual meadow openings or areas of recent invasion), restoration treatments, and fire in particular, had a destabilizing effect, locally eliminating or reducing the cover of disturbance-sensitive meadow species (Appendix S1: Table S2).

For composition, the lack of subplot movement into the RM hull is consistent with the slow rates of colonization of most meadow specialists. In this system, as in many degraded grasslands, most meadow species are absent from the soil seed bank (Lang and Halpern 2007); thus, colonization hinges on dispersal from local or more distant seed sources (Bakker and Berendse 1999, Bossuyt and Hermy 2003, Bisteau and Mahy 2005, Lett and Knapp 2005, Helsen et al. 2013). However, there may be additional barriers to recolonization, including preemption of space or resources by initial colonists (Hulvey and Aigner 2014, Grman et al. 2015, Kraft et al. 2015). We consider these barriers, below, in the context of fire and its interaction with past tree influence (see *Discussion: Effects of fire and past tree influence*).

For structure, we observed notable movement of subplots into the RM hull as a small group of disturbance-adapted meadow generalists compensated for the absence of meadow specialists. These generalists included grasses and forbs with high rates of seed production and effective dispersal (*Bromus carinatus*, *Elymus glaucus*, and *Cirsium remotifolium*) or forbs with rapid clonal growth (*Fragaria* spp.). These taxa were so successful after tree removal that they emerged as treatment, rather than as reference meadow, indicators. In sum, where seed limitation or other barriers prevent the

colonization of grassland specialists (Stampfli and Zeiter 1999, Pywell et al. 2003, Helsen et al. 2013), compensatory establishment by more vagile, disturbance-adapted, generalists can facilitate structural reassembly.

It remains unclear whether “successful” reassembly of community structure implies that treated sites are functionally equivalent to reference sites. The growth-form metrics used in this study are insensitive to species’ identities, including the absence of meadow specialists. Although for some ecological traits or functions, species’ redundancy can compensate for loss of rarer taxa, the broader ecosystem consequences of species’ loss are often poorly understood (Zavaleta and Hulvey 2004, Mouillot et al. 2013, Jain et al. 2014). For example, alteration or loss of meadow habitat to encroachment could affect the diversity or stability of plant–pollinator networks (Winfree et al. 2009, Potts et al. 2010). Recent studies suggest, however, that these networks are fairly resilient due to their dominance by far-ranging generalist pollinators (Helderop 2015; Jones et al., *in press*). In this sense, structural reassembly may restore a critical ecosystem service, despite a difference in composition. However, for ecological functions that are linked to particular species or plant traits, assessing restoration success may require the use of compositional or other trait-based metrics. A fundamental challenge to the science and practice of restoration is to identify traits and ecological functions that are missing in reassembling communities and to determine what limits or enhances their reestablishment (Brudvig and Mabry 2008, Laughlin 2014, Brudvig et al. 2017). Our ability to assess the functional outcomes of reassembly in this system would



TABLE 3. Species' associations with reference meadows (RM) or experimental treatments (UB or B) at final sampling based on indicator species analysis.

Species	Growth form	IV <sub>max</sub>	P
Reference meadow indicators			
<i>Danthonia intermedia</i>	grass	<b>89.3</b>	<b>0.0002</b>
<i>Festuca idahoensis</i>	grass	<b>84.3</b>	<b>0.0002</b>
<i>Lupinus latifolius</i>	forb	<b>76.9</b>	<b>0.0002</b>
<i>Phlox diffusa</i>	subshrub	<b>59.6</b>	<b>0.0002</b>
<i>Achillea millefolium</i>	forb	<b>50.8</b>	<b>0.0002</b>
<i>Erigeron aliceae</i>	forb	<b>42.5</b>	<b>0.0002</b>
<i>Achnatherum occidentale</i>	grass	<b>47.1</b>	<b>0.0002</b>
<i>Viola bakeri</i>	forb	<b>41.6</b>	<b>0.0002</b>
<i>Hieracium scouleri</i>	forb	<b>38.7</b>	<b>0.0002</b>
<i>Elymus repens</i>	grass	<b>37.8</b>	<b>0.0002</b>
<i>Agooseris aurantiaca</i>	forb	<b>37.7</b>	<b>0.0002</b>
<i>Orthocarpus imbricatus</i>	forb	<b>37.6</b>	<b>0.0002</b>
<i>Penstemon procerus</i>	subshrub	17.3	0.0002
<i>Comandra umbellata</i>	subshrub	18.5	0.002
<i>Iris chrysophylla</i>	forb	18.2	0.28
<i>Eurybia radulina</i>	forb	14.6	0.006
<i>Poa pratensis</i> †	grass	14.5	0.0002
<i>Calochortus subalpinus</i>	forb	6.8	0.25
<i>Pteridium aquilinum</i>	forb	5.8	0.006
Unburned (UB) treatment indicators			
<i>Fragaria vesca</i> /F. virginiana	forb	<b>58.1</b>	<b>0.0002</b>
<i>Elymus glaucus</i>	grass	<b>46.2</b>	<b>0.0002</b>
<i>Bromus carinatus</i>	grass	<b>42.4</b>	<b>0.0002</b>
<i>Symphyotrichum spathulatum</i> var. <i>spathulatum</i>	forb	10.0	0.26
<i>Eucephalus ledophyllus</i> var. <i>ledophyllus</i>	forb	7.2	0.003
<i>Anaphalis margaritacea</i>	forb	6.2	0.004
Burned (B) treatment indicators			
<i>Vicia americana</i>	forb	<b>43.5</b>	<b>0.0002</b>
<i>Carex inops</i> ssp. <i>inops</i>	sedge	<b>43.2</b>	<b>0.0002</b>
<i>Cirsium remotifolium</i>	forb	<b>38.5</b>	<b>0.0002</b>
<i>Lathyrus nevadensis</i>	forb	19.3	0.003
<i>Microsteris gracilis</i>	forb	6.8	0.01

Notes: A total of 30 of the 43 species were frequent enough to test (Appendix S1: Table S2). Boldface type denotes a significant indicator ( $P \leq 0.05$  and  $IV_{\max} > 25$ ; see *Methods: Analyses*). Nomenclature follows USDA Plants (<https://plants.usda.gov>).

† Nonnative.

benefit from a more complete understanding of the diversity and level of redundancy of ecological functions provided by meadow generalists and specialists.

#### *Effects of fire and past tree influence*

We hypothesized several possible outcomes of fire (Fig. 1a). It could ( $H_2$ ) promote reassembly (e.g., by enhancing resource conditions or reducing competition from residual forest herbs); ( $H_3$ ) inhibit reassembly (e.g., by reducing survival and local dispersal of desired species); or ( $H_4$ ) vary in its effects, contingent on past tree influence. Among the numerous metrics considered, there

was little evidence that fire promoted reassembly ( $H_2$ ). Although fire can enhance the availability of mineral N in forest and grassland soils (Hobbs and Schimel 1984, Wan et al. 2001), any such benefit was transient, limited to the first growing season after burning (Halpern et al. 2012). Similarly, any reduction in forest herb cover by fire was small compared to that due to tree removal. In contrast, there was strong evidence that fire had adverse effects, consistent with  $H_3$  and  $H_4$ . For example, fire strongly inhibited subplot movement into the RM structural hull. Without fire, subplot presence within the hull increased by >60% by final sampling; with fire it declined by >20%. In areas of limited tree influence, fire also had a destabilizing effect, causing many more burned than unburned subplots to become more distant from RM, both compositionally and structurally.

Mechanistically, fire had both direct and indirect effects on the process of reassembly. First, it reduced the presence and abundance of key reference meadow indicators across the range of encroachment states. For example, the dominant bunchgrass, *Festuca idahoensis*, and many forbs in the Asteraceae were locally extirpated or greatly reduced in abundance (20–65% reductions in frequency, 65–85% reductions in cover). Burning under uncharacteristically high fuel loads likely exceeded the temperature or heating thresholds of these grassland species (Levitt 1980, Antos et al. 1983, Pyke et al. 2010). Moreover, plants depleted of carbohydrate reserves by decades of shading (Celis et al. 2017) were less likely to resprout after fire.

Second, fire had a strong indirect effect on reassembly, particularly in areas where greater tree influence had degraded the meadow flora. Here, burning stimulated germination of the native sedge, *Carex inops* ssp. *inops*, one of the few meadow species with a persistent seed bank (Lang and Halpern 2007). In the absence of competitors, two traits of *Carex*, vigorous rhizomatous spread and production of a deep thatch layer, prevented further colonization, even by generalist forbs and grasses that readily established elsewhere (Halpern et al. 2016). It remains unclear whether these monocultures will persist as a novel community state (Schröder et al. 2005, Fukami and Nakajima 2011) or will gradually be colonized by other meadow species. In a number of systems, long-lived clonally reproducing species can monopolize space or resources after disturbance, stalling community reassembly indefinitely (Royo and Carson 2006, Young and Peffer 2010). The inhibition of reassembly by *Carex* in this system illustrates how site history (long-term degradation of grassland by trees) and disturbance may interact with the regenerative traits of native species to promote “invasive” behaviors that are more often associated with non-natives (Spyreas et al. 2010, Carey et al. 2012).

#### *Convergence within experimental plots*

Experimental subplots converged in composition, irrespective of burn treatment, consistent with  $H_5$ . The

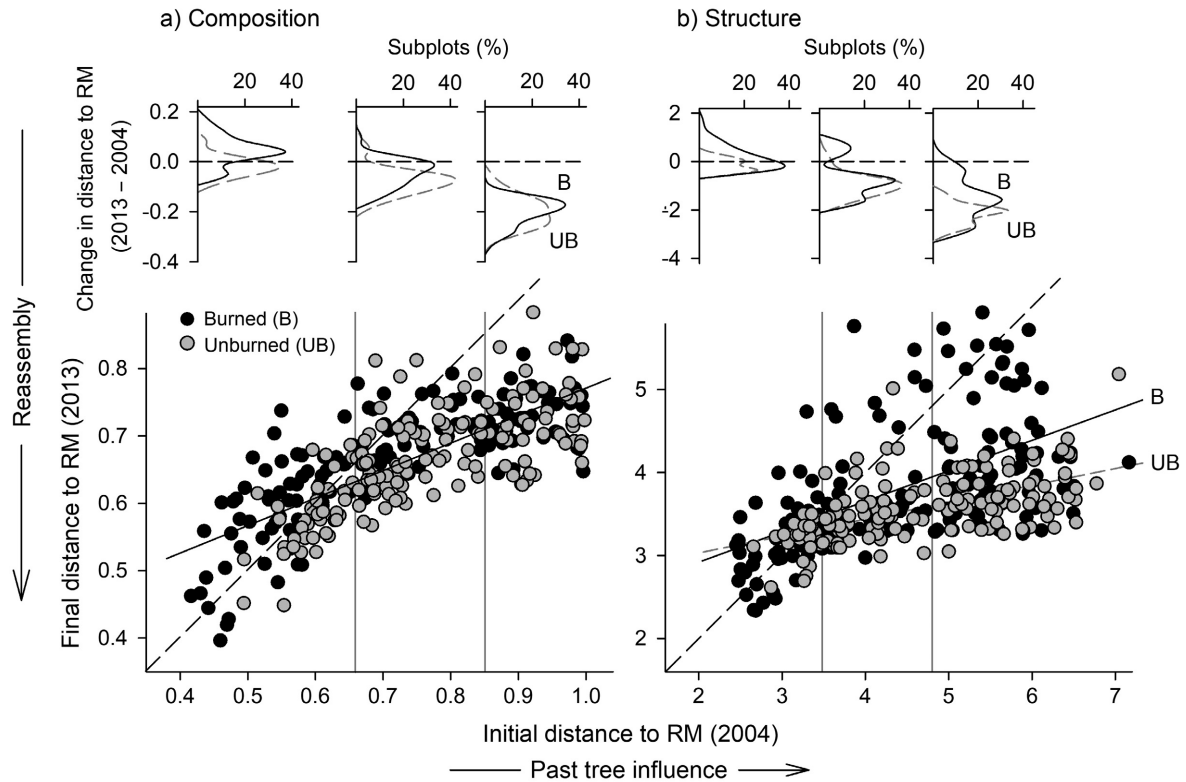


FIG. 5. (a) Compositional and (b) structural distances of experimental subplots from reference meadow (RM) transects at final sampling as a function of initial distance (past tree influence) and burn treatment (UB or B). Values above the dashed 1:1 line represent increases in distance; values below the line represent decreases (reassembly). Regression slopes differ between UB and B for structure but not for composition. See Appendix S1: Table S4 for linear mixed-model results. Frequency histograms summarize changes in distance among similar-sized groups of subplots characterized by initially small, moderate, or large initial distances from RM (groups separated by vertical gray lines).

species driving convergence were the same meadow generalists, or “treatment indicators,” responsible for the progression of subplots toward reference meadows. High rates of seed production and effective dispersal contributed to their ubiquitous colonization (90–100% of subplots; Appendix S1: Table S2). That meadow generalists were not more restricted in their distributions suggests that any tree-induced variation in soil chemical or microbial properties (Griffiths et al. 2005) had dissipated after trees were removed, or that colonists were insensitive to this variation—a sharp contrast to the persistence of soil legacies in other tree-invaded grasslands (Stahlheber et al. 2015). It is possible that species composition will diverge among subplots in the future if subsequent colonists (e.g., meadow specialists) have narrower or differing resource requirements (Lepš and Rejmánek 1991, Matthews and Spyreas 2010) or if their seed sources are spatially segregated and dispersal is poor (Chase 2003).

In contrast to the compositional trend, burned subplots failed to converge in structure, consistent with  $H_7$  (tempering of convergence by fire). Mechanistically, the absence of growth-form convergence reflects the strong interaction of fire with initial vegetation state, promoting herb and grass dominance over most of the

encroachment gradient, but sedge dominance in areas of greater tree influence. That we failed to detect convergence of structure, but not of composition, likely reflects the greater contribution of sedge cover to the structural metric (as one of six growth-form variables) than to the compositional metric (as one of 30 species).

#### CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Our study addresses the challenges of restoring ecological systems that have undergone fundamental changes in vegetation state (Hobbs et al. 2006, MacDougall and Turkington 2007, Suding and Hobbs 2009, MacDougall et al. 2013, Ratajczak et al. 2016). Despite uncertainty about the historical role of fire and possible triggers of recent invasions, resource managers are using prescribed burning as a tool for grassland restoration. The practice reflects the perceived importance of fire as a natural disturbance process and the need to dispose of woody fuels following tree removal. The broadcast vs. pile-burn treatments used in this experiment test both objectives in tandem.

Our results provide strong evidence that broadcast burning after tree removal does not aid, but can slow or

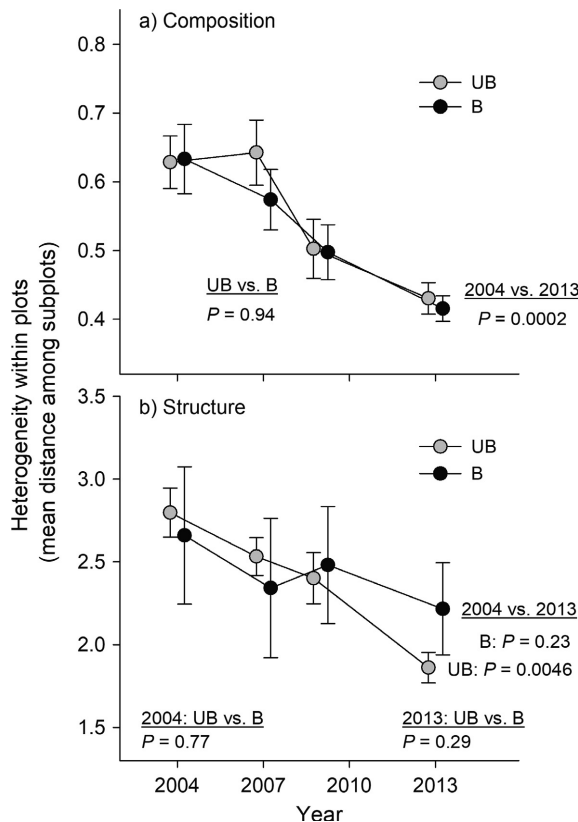


FIG. 6. (a) Compositional and (b) structural heterogeneity within plots as a function of time and burn treatment (UB vs. B). Values are treatment means ( $\pm 1$  SE;  $n = 3$  plots). For composition,  $P$  values are from linear mixed models testing effects of time (2013 vs. 2004), treatment, and their interaction (non-significant). For structure,  $P$  values are from post-hoc comparisons between treatments or within treatments (initial vs. final sampling), following a significant time  $\times$  treatment interaction. For the full set of mixed-model results, see Appendix S1: Table S5.

divert recovery of native grasslands. Interestingly, these adverse effects are not mediated by nonnative or woody species, as in other degraded grasslands (D'Antonio 2000, Stanley et al. 2011, MacDougall et al. 2013, Stahlheber et al. 2015), but by the direct and indirect effects of fire on the resident herbaceous flora itself. On the other hand, responses to tree removal demonstrate that alternative treatments can be as, or more effective than fire, if they modify resource conditions to favor the establishment or growth of desired species (MacDougall and Turkington 2007, but see Scholtz et al. 2018). Yet, from an operational or risk-management perspective, some form of burning may be desirable or necessary to dispose of woody residues. In this system, we demonstrated that pile burning (leaving 90% of the ground surface unburned) can be an efficient and effective method of disposal: burn scars recovered rapidly, aided by the soil-mixing activities of gophers, the rapid colonization of disturbance-adapted meadow generalists, and the

limited propagule pressure of exotics (Halpern et al. 2014). In systems in which burn scars are more persistent or susceptible to invasion by exotics, additional intervention may be necessary (Haskins and Gehring 2004, Korb et al. 2004, DeSandoli et al. 2016).

Our experiment is unique in testing the range of conditions (initial vegetation states) over which treatments might be effective or lead to undesirable results. In the absence of fire, we observed stronger positive responses to tree removal in areas of greater tree influence. Alford et al. (2012) reported a similar response to removal of redcedar from tallgrass prairies, with greater increases in herbaceous diversity in areas of greater tree cover. Although recovery of the original grassland state may be difficult once woody plants establish (Heisler et al. 2003, Briggs et al. 2005, Lett and Knapp 2005), our system does not appear to have passed this threshold (Ratajczak et al. 2016), even after multiple centuries of tree influence. Despite the abundance of tree seed, conifer reinvasion remains sparse, largely restricted to the edges of plots (Kremer et al. 2014). Nevertheless, reassembling communities retain strong legacies of past tree influence evident in the reduced cover and diversity of meadow species, including meadow specialists. The management implications of our work are clear: targeting restoration early in the invasion process reduces the loss of desired species, the cost and feasibility of fuel reduction, and the adverse effects of fire.

Numerous factors may dictate longer-term patterns of reassembly, but two are likely to figure prominently in this system: the extent to which meadow specialists are seed limited (due to low production or poor dispersal) and ongoing preemption by *Carex*. With the exception of *Carex*-dominated subplots, the greater availability of open space in treated vs. reference sites suggests that recruitment is limited more by seeds than by safe sites. Loss of local seed sources to burning has likely exacerbated this condition, although seed sources are also present in neighboring meadows. For species that produce few seeds or are poor dispersers (Pywell et al. 2003, Kirkman et al. 2004), recolonization may simply require more time. The proximity of high-quality habitat in the surrounding landscape should facilitate passive immigration, in contrast to the strong dispersal barriers that characterize highly fragmented or isolated grasslands (Dzwonko and Loster 2007, Damschen et al. 2008, Brudvig 2011, Helsen et al. 2013). At the same time, local persistence of the *Carex*-dominated state may stall reassembly indefinitely, even if seed is not limiting.

Understanding the mechanisms that contribute to reassembly outcomes, including site history, landscape setting, and the context-dependence of treatment effects, represents a fundamental challenge to restoration science (Grman et al. 2013, Brudvig et al. 2017). We demonstrate that tree removal from mountain grasslands can reverse the effects of decades to multiple centuries of encroachment, although legacies of past tree influence persist in the composition and structure of

reassembling communities. Prescribed fire both slows and, in some instances, stalls reassembly by reducing survival or altering the competitive balance among resident meadow species. Thus, treatments designed to mimic natural disturbance processes can have adverse effects, depending on the contexts in which they are applied. Our results highlight the distinction between disturbance processes that maintain ecosystem stability and those that are critical or limiting to reassembly following a change in state.

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## SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1860/full>

## DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.v5f76v4>