Past tree influence and prescribed fire mediate bioticinteractions and community reassembly in agrassland-restoration experiment

Past tree influence and prescribed fire mediate biotic interactions and community reassembly in a grassland-restoration experiment

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Summary

1. Woody plant encroachment of grasslands is occurring globally, with profound ecological consequences. Attempts to restore herbaceous dominance may fail if the woody state is resilient or if intervention leads to an alternate, undesirable state. Restoration outcomes often hinge on biotic interactions – particularly on priority effects that inhibit or promote community reassembly.

2. Following experimental tree removal from conifer-invaded grasslands, we documented substantial variation in community reassembly associated with the changing abundance of the native clonal sedge *Carex inops* L.H. Bailey subsp. *inops*. We explored possible mechanisms for this variation, focusing on the nature and timing of interactions between the meadow community and *Carex* and on how past tree influence and prescribed fire mediate the outcomes of these interactions.

3. Meadow species increased after tree removal, but less so in burned than in unburned plots. *Carex* expanded dramatically after fire, particularly where past tree influence had been greater.

4. Meadow species and *Carex* developed an increasingly negative association over time; pre-emption was reciprocal, but offset in time and space. Meadow species inhibited *Carex* through vegetative recovery in areas of limited or recent tree influence, irrespective of fire. *Carex* inhibited meadow reassembly in areas of greater tree influence, but only with burning.

5. *Synthesis and applications.* Tree removal and fire imposed across a range of altered meadow states yielded varying outcomes, reflecting biotic interactions and species' regenerative traits that inhibited or promoted reassembly. Fire tended to destabilize the remnant meadow community and, in areas more degraded by encroachment, stimulated release of *Carex*, which inhibited reassembly. Knowledge of the context dependence of biotic interactions can enhance the effectiveness of restoration by establishing the bounds within which treatments produce desirable or undesirable outcomes.

Key-words: burning, competition, inhibition, meadow restoration, pre-emption, priority effects, species' interactions, tree encroachment

Introduction

Regime shifts, transitions from one ecosystem state to another, can have profound, often undesirable consequences for biological diversity and other ecosystem services (Scheffer *et al.* 2001; Folke *et al.* 2004). Ecological restoration seeks to reverse these changes and to promote reassembly of the desired state. Attempts at restoration

may fail, however, if the altered state is resilient or if intervention leads to an unexpected, equally resilient state (Mayer & Rietkerk 2004; Suding, Gross & Houseman 2004; Suding & Hobbs 2009). Biotic interactions play a critical role in this process. Notably, priority effects, in which initial colonists pre-empt space or resources from later arrivals, can shape the outcomes of community reassembly (Belyea & Lancaster 1999; Young, Chase & Huddleston 2001; Martin & Wilsey 2012). Pre-emption is more likely if initial colonists have traits that ensure rapid

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establishment and growth (e.g. high fecundity and early phenology). These traits may contribute to persistence of exotic species in degraded ecosystems and to the difficulty of restoring native composition (Dickinson, Hopwood & Wilsey 2012; Wainwright, Wolkovich & Cleland 2012; Wilsey, Barber & Martin 2015). However, native species may also impede community reassembly if their traits (e.g. strong clonality and long life span; Royo & Carson 2006; Young & Peffer 2010) confer a competitive advantage after disturbance. Using an experiment designed to reverse the effects of a regime shift from grassland to forest, we explore how variation in pre-treatment context (reflecting the cumulative influence of trees) and disturbance (fire) interact with the regenerative traits of species to alter biotic interactions and the outcomes of restoration.

Woody plants are expanding into grasslands world-wide (Scholes & Archer 1997; Van Auken 2000; Eldridge *et al.* 2011), altering the biodiversity, ecosystem services and human uses of these systems (Jackson *et al.* 2002; Ratajczak, Nippert & Collins 2012; Sala & Maestre 2014). Encroachment is often reinforced by positive feedbacks that confer resilience on the woody state (Archer *et al.* 1988; Ratajczak *et al.* 2011), thereby limiting the effectiveness of restoration (Heisler, Briggs & Knapp 2003; Briggs *et al.* 2005). Even with successful removal of woody plants, grassland reassembly can be delayed by legacy effects (Lett & Knapp 2005). Experiments to reverse effects of encroachment – either through mechanical removal or burning – are thus useful for understanding the factors that constrain reversal of the altered state and reassembly of the desired state (Alford *et al.* 2012; Ratajczak *et al.* 2014).

Conifer encroachment threatens persistence of montane grasslands (or meadows) throughout western North America. In the Oregon Cascade Range, montane meadows that historically occupied a small portion of the landscape have contracted dramatically (>50%) in the 20th century (Takaoka & Swanson 2008) due to changes in climate, grazing pressure and fire frequency (Vale 1981; Miller & Halpern 1998), and to positive feedbacks that promote tree establishment (Halpern *et al.* 2010). At Bunchgrass Ridge, the site of the only large-scale meadow restoration experiment in western North America (Halpern *et al.* 2012), two centuries of invasion by *Pinus contorta* Douglas ex Loudon and *Abies grandis* (Douglas ex D. Don) Lindl have created a fine-scale mosaic of encroachment states (see Fig. S1, Supporting Information), including residual meadow openings and forests of increasing age (and dominance by *Abies*) from which meadow species have been progressively lost (Haugo & Halpern 2007, 2010). The mosaic of vegetation states provides an ideal setting for exploring the dependence of community reassembly on the degree to which meadows have been altered by trees.

The experiment tests responses to tree removal – with or without fire – as influenced by initial vegetation state. The fire treatments compare two methods of slash disposal (important for reducing fire risk): broadcast vs. pile burning, the latter, leaving most of the ground surface unburned. They also test the ecological effects of fire in a system in which natural ignitions are uncommon and the history of anthropogenic burning is poorly understood.

Initial (3-year) responses to tree removal included a marked shift in dominance from forest understorey to meadow species – both with and without fire (Halpern *et al.* 2012). Longer term (8-year) responses, however, suggest a decelerating but variable pace of reassembly, coincident with expansion of a native meadow sedge, *Carex inops* (Fig. S2). Initially positive associations between *Carex* and co-occurring meadow species have shifted to strongly negative, suggesting inhibition of meadow reassembly by *Carex*. Here, we use the full set of experimental data – collected at fine spatial and temporal resolution – to model the timing and strength of interactions between *Carex* and meadow species, and how these are mediated by initial community state (indicative of past tree influence) and fire. We suggest that the combined negative effects of tree influence and fire interact with the regenerative traits of *Carex* to alter the outcomes of community reassembly.

Materials and methods

STUDY AREA

Bunchgrass Ridge forms a high-elevation plateau (~1350 m) along the western edge of the High Cascade Province in Oregon (USA). Soils are deep, fine to very fine sandy loams, originating from andesitic basalt and tephra. Soil profiles suggest grassland dominance for centuries or possibly millennia (D. Lammers, personal communication). The climate is maritime, with cool, wet winters and warm, droughty summers. Temperature averages –6·9 °C (min) and 0·7 °C (max) in January and 6·1 °C and 27·8 °C in July (data from Santiam Pass, 1488 m; Western Regional Climate Center; http://www.wrcc.dri.edu/summary/climsmor.html). Annual precipitation averages ~220 cm but is highly seasonal: only 7·5% occurs in the growing season; most falls as snow, which can persist into May or early June.

The 100-ha study area supports a fine-scale mosaic of encroachment states reflecting the progressive, but patchy, invasion of natural meadows by *Pinus contorta* and *Abies grandis* over the past two centuries (Fig. S1; Halpern *et al.* 2010). Extensive infilling since ~1950 has reduced meadow extent by >50%; details of the invasion history are presented in Halpern *et al.* (2010).

Uninvaded meadows support diverse communities of perennial forbs and graminoids characteristic of mesic and dry meadows throughout the Cascade Range (McCain, Halpern & Lovtang 2014). Once conifers invade, however, cover and diversity of meadow species predictably decline as forests age and open-canopied *Pinus* is replaced by denser canopied and longer lived *Abies* [see details in Haugo & Halpern (2007); reproduced in Table S1]. The strong relationship with encroachment state makes it possible to use cover of meadow species as a proxy for past tree influence when age structure data are lacking (see *Analyses*).

Carex inops, the dominant sedge in this system, is common in meadows and open forests throughout the Cascade Range (McCain, Halpern & Lovtang 2014). It is a caespitose perennial with persistent leaves, vigorous rhizomes and dense fibrous roots. Among meadow species, it is relatively tolerant of shade, persisting for decades after tree establishment, albeit at low cover (Haugo & Halpern 2007; Table S1). It is one of few meadow species present in the soil seed bank (Lang & Halpern 2007).

Although fire may have contributed to the origin and maintenance of mountain meadows historically, natural ignitions are infrequent (>100 years; Weisberg & Swanson 2003). In some areas, Native Americans and European settlers burned to maintain natural meadow openings and edges (Burke 1979; Boyd 1999). Within the study area, however, there is no evidence of fire of sufficient severity over the last two centuries to have caused scarring of trees (Halpern *et al.* 2010). Grazing of meadows by domestic sheep was common in the Cascades in the late 1800s and early 1900s (Johnson 1985) although the history (timing and intensity) of grazing at Bunchgrass Ridge is unknown.

EXPERIMENTAL DESIGN

We used aerial photos and field reconnaissance to delineate a 16-ha area of conifer-invaded meadow for experimentation. Within it, we established nine 1-ha plots (experimental units; Fig. S3), each containing a fine-scale mosaic of remnant meadow openings and forest patches of differing ages (Figs S1 and S3; Halpern *et al.* 2010). Each plot was randomly assigned to one of three treatments (*n* = 3): Control (C), no trees removed; Unburned (UB), all trees removed with logging residues piled and burned, leaving 90% of the ground surface unburned; and Burned (B), all trees removed with logging residues broadcast burned (see Appendix S1 for details on treatments). Here, we consider only the tree-removal plots (UB and B).

FIELD METHODS

Prior to treatment, we established a grid system in each plot to delineate 100, 10 × 10 m subplots (Fig. S1). In a subset of these, we aged all trees >1·4 m tall (Halpern *et al.* 2010) and quantified the relationships between age structure and meadow species abundance and diversity using pre-treatment vegetation data (Table S1; Haugo & Halpern 2007).

In each of the six tree-removal plots, we selected either 32 or 64 subplots (160 per treatment) to sample vegetation responses to experimental treatments. We sampled before tree removal (2004) and 1, 3 and 7 years after burning (2007, 2009 and 2013). At each sampling date, cover (%) of each species was visually estimated in four 1 × 1 m quadrats spaced 1 m apart along a diagonal transect of each subplot. Estimates of species cover were independent, thus could sum to >100% in a quadrat. In burned (B) subplots, burn severity was quantified in 2007 as the total cover of white ash, blackened duff and charcoal (≤100%). In 2013, we also sampled 16 'reference meadows' – uninvaded meadows contiguous with or adjacent to the experimental plots (Fig. S3) – having topography, soils and species composition comparable to remnant meadow openings within the plots. Within these, we sampled 117 transects using the same quadrat design as in the experimental subplots.

ANALYSES

Prior to analyses, we classified species based on habitat affinity: forest understorey (*n* = 55), meadow (*n* = 49) and ruderal (*n* = 22) (Halpern *et al.* 2012). Ruderals and a set of 16 unclassified species contributed minimally to the vegetation (combined cover <1%) and were dropped from the analyses. Within each quadrat, we summed the cover and tallied the number of forest understorey and meadow species (excluding *Carex*). Quadrat values were averaged for each subplot and reference meadow transect.

In this study, we treat subplots as independent samples: they are separated by distances of >10 m (much larger than the sizes of interacting species), they showed significant and large variation in past tree influence (pre-treatment cover of meadow species), and they represent the scale at which *Carex* and co-occurring meadow species interact.

We used frequency histograms to characterize the changing distributions of cover and richness of *Carex*, meadow and forest species among subplots representing the two treatments (*n* = 160 per treatment). We used two-samples KS tests to determine whether: (i) distributions changed in response to treatment (2004 vs. 2013), (ii) distributions differed between treatments at final sampling and (iii) distributions differed between treatments and reference meadows. We also conducted Welch two-samples *t*-tests (*n* = 3, assuming unequal variance) to determine whether treatments differed in their median values of cover and richness at final sampling (they did not differ prior to treatment).

We used ANCOVA to assess the relationship between past tree influence (using pre-treatment cover of meadow species as a proxy) and final abundance of both meadow species and *Carex* (*n* = 160 subplots per treatment), and whether this relationship differed between treatments (testing for differences in slope).

To illustrate the changing associations of meadow species and *Carex*, we produced bivariate plots of meadow cover or richness vs. *Carex* for both treatments at initial (2004) and final (2013) sampling (*n* = 160 subplots per treatment). For each comparison, we computed the Pearson correlation coefficient. The same relationships were tested among transects representing uninvaded reference meadows (*n* = 117).

We used multiple regression models to explore whether biotic interactions could explain the changing relationships between meadow species and *Carex*. For each post-treatment measurement (*t*), we regressed meadow cover, meadow richness, and *Carex* cover on meadow, *Carex,* and forest understorey cover at the previous measurement (*t*−1) (or, for the richness model, on meadow richness at *t*−1) (*n* = 160). Models thus tested responses to the competitive environment 2–4 years earlier, while accounting for temporal autocorrelation in the response. Given the complexity of these models and the contrasting responses to treatments, we analysed treatments separately. The random effect of plot (within which subplots were nested) had little or no effect on model fit, thus was excluded from final models. Models for the burned treatment also tested the effects of burn severity. We initially included multiway interactions among predictors, but all were non-significant (*P* > 0·05).

Standard diagnostics were used to evaluate adherence to the assumptions of regression (normality and homoscedasticity of residuals). With raw cover, there were small departures from these assumptions. We did not view these as problematic, however, because we did not test the significance of regression coefficients or full models, avoiding the need to adjust alpha levels

(Harrell 2001). Raw and log-transformed values produced similar results; thus, we based analyses on the former to simplify interpretation.

For each model, we began with all predictors and used backward elimination, selecting as the final model that with the highest adjusted R^2. We tested an analogous process using AIC, which produced the same sets of predictors. Thus, we report adjusted R^2, which provides a clearer measure of absolute goodness-of-fit and is easier to compare among models. For each model, we computed standardized regression coefficients (β) and partial correlation coefficients (*pr*) between each predictor ($t-1$) and the response (t). In combination, the full set of models was used to assess changes in nature, timing and strength of interaction between meadow species and *Carex* – inferring pre-emption from the negative effect of a predictor on the subsequent response, and vegetative persistence from significance of the temporal autocorrelation of meadow species or *Carex*. Analyses were conducted in R ver. 3.0.3 (R Core Team 2014).

Results

CHANGES IN THE DISTRIBUTIONS OF ABUNDANCE AND RICHNESS WITH TREATMENT (+/−FIRE)

Prior to tree removal (2004), meadow species and *Carex* were notably less abundant in the experimental subplots than in reference meadows, although there was considerable variation among subplots (Fig. 1). Tree removal resulted in large declines in forest species (Fig. S4) and correspondingly large increases in both meadow species and *Carex* ($P < 0.0001$ for KS tests of 2004 vs. 2013 distributions), although distributions of cover and richness differed between treatments at final sampling ($P < 0.0001$ for KS tests of UB vs. B in 2013) (Figs 1 and S4).

Cover of meadow species increased more frequently in UB than in B (81% vs. 53% of subplots). Median cover of meadow species more than tripled in UB (to 33·5%) and nearly doubled in B (to 22·4%) (UB vs. B, $t = 3.27$, $P = 0.03$), but it remained substantially lower than in reference meadows (63·3%) (Figs 1a–c). Richness also increased more frequently in UB than in B (92% vs. 63% of subplots). Median richness was only marginally greater in UB than in B (5·3 vs. 4·5 species per quadrat; $t = 2.87$, $P = 0.099$), but remained considerably lower than in reference meadows (9·8) (Figs 1a–c).

Carex expanded in most subplots (82% of B, 71% of UB). At final sampling, median cover was nearly three times greater in B than in UB (25·3% vs. 9·2%; Figs 1d, e), although the difference was not significant at the scale of plots ($t = -1.67$, $P = 0.19$). Median cover in B was also much greater than in reference meadows (11·0%; Figs 1e,f). *Carex* cover exceeded its maximum value in reference meadows (43%) in 21% of B, but only in 7% of UB subplots.

Forest understorey species declined dramatically in both treatments (96–98% of subplots) (Fig. S4). Median

cover was reduced by >80% in UB and >90% in B; richness was reduced by 65% in UB and 80% in B. Differences between treatments were non-significant for both cover ($t = 1.02$, $P = 0.42$) and richness ($t = 2.81$, $P = 0.11$).

INTERACTION BETWEEN CUMULATIVE TREE INFLUENCE AND FIRE

Past tree influence (expressed by pre-treatment cover of meadow species) mediated responses to fire (Fig. 2). For meadow species, final cover was positively correlated with pre-treatment cover (Fig. 2). Burning did not affect the slope of the relationship (non-significant interaction with treatment, $F = 0.15$, $P = 0.70$), but it reduced cover by ~40% relative to the unburned treatment. The 'reassembly deficit' – the distance between fitted cover in experimental subplots and median cover in reference meadows – was positively correlated with tree influence and magnified by fire (Fig. 2).

For *Carex*, final cover was negatively correlated with pre-treatment meadow cover in B, but not in UB (significant interaction with treatment, $F = 19.05$, $P < 0.001$; non-significant slope for UB, $t = -1.46$, $P = 0.14$). Relative to reference meadows, *Carex* showed little or no increase in UB, but progressively greater increase with past tree influence in B (Fig. 2). For example, where pre-treatment meadow cover exceeded 30% (areas of limited tree influence), *Carex* showed little response (median increase of ~2% cover). Where pre-treatment meadow cover was less (areas of greater tree influence), *Carex* expansion was dramatic (median increase of 25% cover and frequently twice that). In combination, tree influence and burning produced strong contrasts in vegetation structure, with meadow species dominating unburned areas with minimal tree influence and *Carex* dominating burned areas greatly altered by trees.

CHANGING RELATIONSHIPS BETWEEN MEADOW SPECIES AND *CAREX*

Before treatment (2004), meadow species and *Carex* were positively correlated (Fig. 3), reflecting similar (negative) responses to encroachment. However, at final sampling (2013), correlations ranged from weakly negative in UB (| r | ≤ 0·14; Figs 3a,d) to strongly negative in B (| r | ≥ 0·48; Figs 3b,e). In reference meadows, correlations were moderately negative (cover; $r = -0.30$; Fig. 3c) or weak (richness, $r = -0.08$; Fig. 3f).

DIRECTION, STRENGTH AND TIMING OF BIOTIC INTERACTIONS

Most variation in meadow cover or richness was explained by previous cover or richness (including the initial post-disturbance response; Table 1). However, the
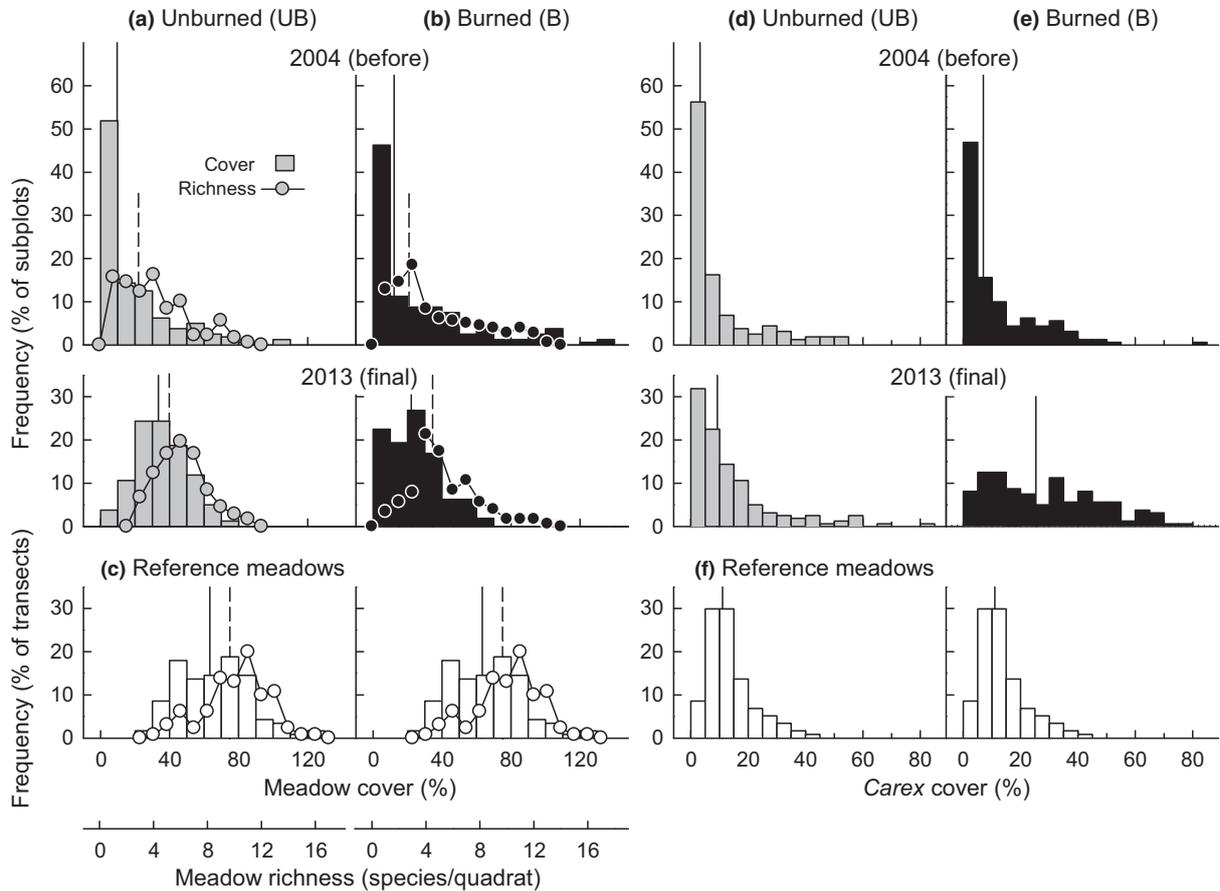
Fig. 1. Frequency distributions of meadow cover and richness (a, b) and *Carex* cover (d, e) before treatment and at final sampling. Reference meadow distributions (c, f) are repeated to aid comparisons with treatments. Vertical lines are median cover (solid) and richness (dashed).
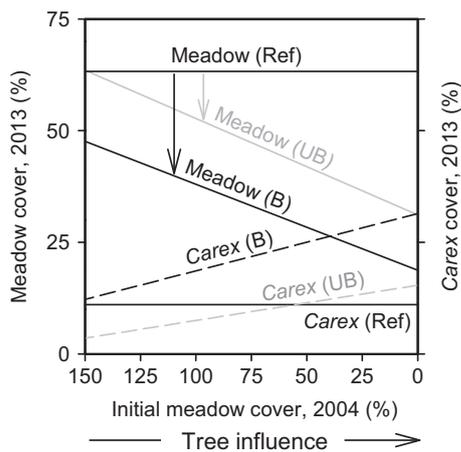

Fig. 2. Meadow and *Carex* cover at final sampling (2013) as functions of tree influence (initial meadow cover, 2004) and fire treatment. Regression lines are fitted relationships; for *Carex* (UB) the slope is non-significant. Horizontal lines are reference meadow medians; vertical arrows represent the 'reassembly deficit'.

relationship with *Carex* switched from initially neutral (B) or weakly positive (UB) (legacies of pre-treatment association) to increasingly negative. Burning both accel-

erated and enhanced this effect (Figs 4a,b; Table 1). The relationship with forest species was also negative, but only in UB where residual cover of forest species was greater (Table 1). Burn severity had an initially negative, but diminishing effect on meadow cover and richness (Table 1).

For *Carex*, most variation in cover was explained by cover at the previous measurement. However, this relationship was much weaker in B than in UB, particularly in the initial post-treatment response (Table 1). The effect of meadow cover on *Carex* switched from initially neutral (UB) or positive (B) to negative, and increasingly so in B (Figs 4c,d; Table 1). Forest species had neutral or weakly negative effects on *Carex* (Table 1). *Carex* responded positively to burn severity (in contrast to meadow species), but its response was delayed (Table 1).

Discussion

Current vegetation patterns support our initial findings: Tree removal can effectively shift dominance from forest understorey to native meadow species, even after more than a century of tree influence (Halpern *et al.* 2012).
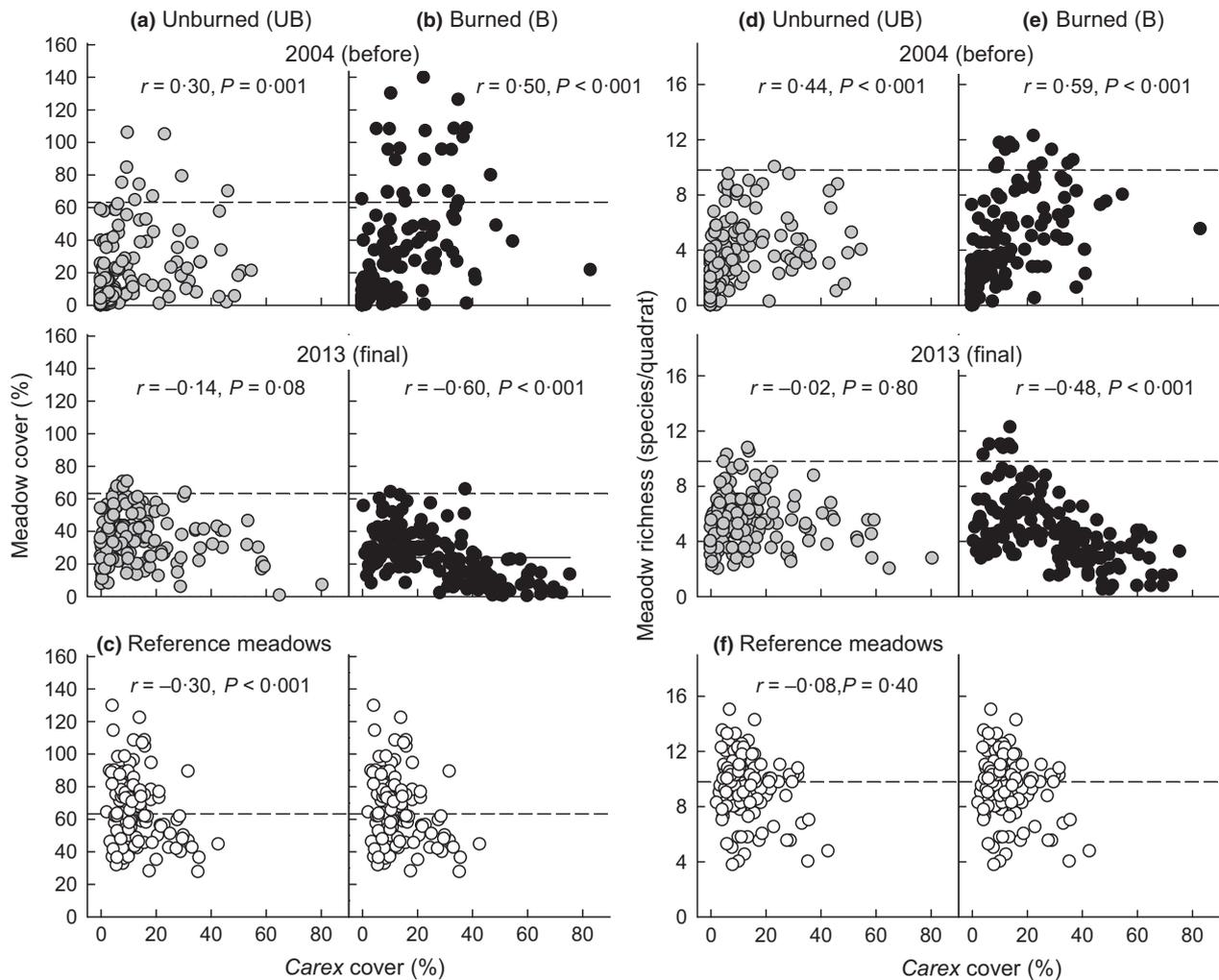
Fig. 3. Relationships of meadow cover (a, b) and richness (d, e) with *Carex* cover before treatment and at final sampling. Reference meadow data (c, f) are repeated to aid comparisons with treatments. *r*, Pearson correlation. Horizontal lines are median cover and richness in reference meadows.

However, recent trends suggest that community reassembly has slowed or stalled: (i) rates of increase in meadow species have declined, and experimental communities have not attained the cover and diversity of reference meadows 8 years after tree removal; (ii) *Carex inops*, the native sedge, has attained uncharacteristically high cover, particularly in burned plots; and (iii) an initially positive association of meadow species with *Carex* has switched to strongly negative. Our analyses suggest that biotic interactions, mediated by effects of encroachment and fire, have contributed to marked variation in the pace of reassembly.

REASSEMBLY OUTCOMES VARY WITH PAST TREE INFLUENCE AND FIRE

Reassembly outcomes varied widely in response to tree removal, reflecting the combined influences of initial vegetation state (past tree influence) and fire. Model results

suggest that successful reassembly in this system hinges on vegetative recovery of surviving plants. Pre-treatment cover and richness of meadow species were strong predictors of initial post-treatment values (Table 1), and pre-treatment cover was a strong predictor of final cover (Fig. 2). Almost all meadow species in this system are perennials with well-developed root systems (rhizomes, caudices or taproots) that enable rapid recovery following soil disturbance or fire. Thus, to the extent that these species persist in the understorey, vegetative recovery is possible. Once they are lost, however, community reassembly hinges on seed dispersal because most meadow species (except *Carex*) are absent from the soil seed bank (Lang & Halpern 2007).

Fire had both direct and indirect effects on community reassembly. It had a strong direct effect, reducing meadow cover and richness, independent of past tree influence, thus contributing to the greater 'reassembly deficit' in burned than in unburned plots (Fig. 2). It

Table 1. Results of multiple regression models predicting responses (*t*) of meadow species and *Carex* from previous cover or richness (*t*−1) and burn severity (summed cover of white ash, blackened duff and charcoal)

| Responses | | | Predictors | | | | | | | | | | Adj. R^2 |
| | | | Carex cover (*t*−1) | | Meadow cover (*t*−1) | | Meadow richness (*t*−1) | | Forest understorey cover (*t*−1) | | Burn severity | | |
Variable (*t*)	Treatment	Year (*t*)	β	*pr*	β	*pr*	β	*pr*	β	*pr*	β	*pr*	
Meadow cover	Unburned (UB)	2007	0·099	0·08	0·790	0·80	–		0·064	0·11	–		0·67
		2009	ns		0·780	0·77	–		−0·082	−0·13	–		0·60
		2013	−0·174	−0·21	0·567	0·58	–		−0·216	−0·26	–		0·37
	Burned (B)	2007	ns		0·648	0·69	–		0·137	0·20	−0·317	−0·43	0·57
		2009	−0·081	−0·12	0·826	0·74	–		ns		−0·163	−0·27	0·74
		2013	−0·231	−0·32	0·654	0·69	–		ns		ns		0·55
Meadow richness	Unburned (UB)	2007	ns		–		0·915	0·92	ns		–		0·84
		2009	ns		–		0·921	0·92	ns		–		0·85
		2013	−0·086	−0·17	–		0·860	0·87	−0·122	−0·23	–		0·75
	Burned (B)	2007	ns		–		0·802	0·83	0·056	0·10	−0·263	−0·45	0·74
		2009	ns		–		0·936	0·94	ns		−0·028	−0·08	0·90
		2013	−0·134	−0·31	–		0·910	0·91	ns		−0·003	−0·01	0·86
Carex cover	Unburned (UB)	2007	0·729	0·73	ns		–		ns		–		0·53
		2009	0·821	0·82	−0·072	−0·23	–		−0·136	−0·12	–		0·68
		2013	0·811	0·82	−0·106	−0·19	–		−0·079	−0·14	–		0·68
	Burned (B)	2007	0·361	0·38	0·382	0·40	–		ns		ns		0·41
		2009	0·567	0·46	−0·376	−0·29	–		−0·096	−0·12	0·325	0·34	0·33
		2013	0·558	0·64	−0·393	−0·50	–		ns		ns		0·56

β, standardized coefficient; *pr*, partial correlation (Pearson correlation for single-predictor models); Adj. R^2, variation explained by full model; ns, not significant; dash, not applicable.

also constrained reassembly indirectly, through a positive effect on *Carex* – contingent on past tree influence (Fig. 2). Two factors likely contribute to localized expansion of *Carex* in burned subplots: a well-developed seed bank (>150 seedlings m^{-2} in pre-treatment emergence trials; Lang & Halpern 2007) and greater severity of fire in areas of greater tree influence (Halpern *et al.* 2012). Regression models for *Carex* suggest differing regenerative mechanisms between treatments. In unburned subplots, post-treatment cover was largely explained by pre-treatment cover, suggesting vegetative persistence through disturbance. However, in burned subplots, where *Carex* showed marked expansion, the correlation with pre-treatment cover was much weaker and burn severity had a positive, but lagged effect, suggesting poorer survival of existing plants and abundant recruitment from the seed bank. With competition greatly reduced, newly emerged seedlings can also exploit the flush of available N common after burning (Wan, Hui & Luo 2001; Halpern *et al.* 2012). Fire thus provides a transient window for establishment (Keeley 1998; Moreno *et al.* 2011), setting the stage for clonal expansion of a highly competitive species in a largely competition-free environment. The combined effects of species' loss and *Carex* expansion in these older, more developed forests pose a particular challenge to community reassembly given the dependence of meadow species on dispersal and recruitment from seed.

CONTRASTING MECHANISMS OF PRE-EMPTION BY MEADOW SPECIES AND *CAREX*

Regression models, quantifying the changing influence of past on current abundance, provide strong evidence of pre-emption during reassembly – both of *Carex* by meadow species and of meadow species by *Carex*. Models reveal significant variation in the distributions of these effects relative to the mosaic of initial vegetation states and fire. Pre-emption of *Carex* by meadow species was more likely in subplots with little tree influence (recent encroachment), irrespective of fire. In contrast, pre-emption of meadow species by *Carex* was more likely in subplots with greater tree influence treated with fire.

Models also highlight variation in the timing of interactions, reflecting underlying differences in the mechanisms of pre-emption. Where meadow species were sufficiently abundant prior to tree removal, they established priority more quickly than did *Carex*. Even in areas of modest cover (30%), vegetative recovery was sufficient to inhibit *Carex* expansion. In contrast, pre-emption by *Carex* was slower, limited by low pre-treatment abundance and the time required for seedlings to develop sufficient cover to pre-empt later arrivals. Once established, however, *Carex* was a strong competitor for space and resources. Vigorous clonal spread, dense systems of fibrous roots and prolific litter production contributed to the development of near-monocultures (Fig. S2).
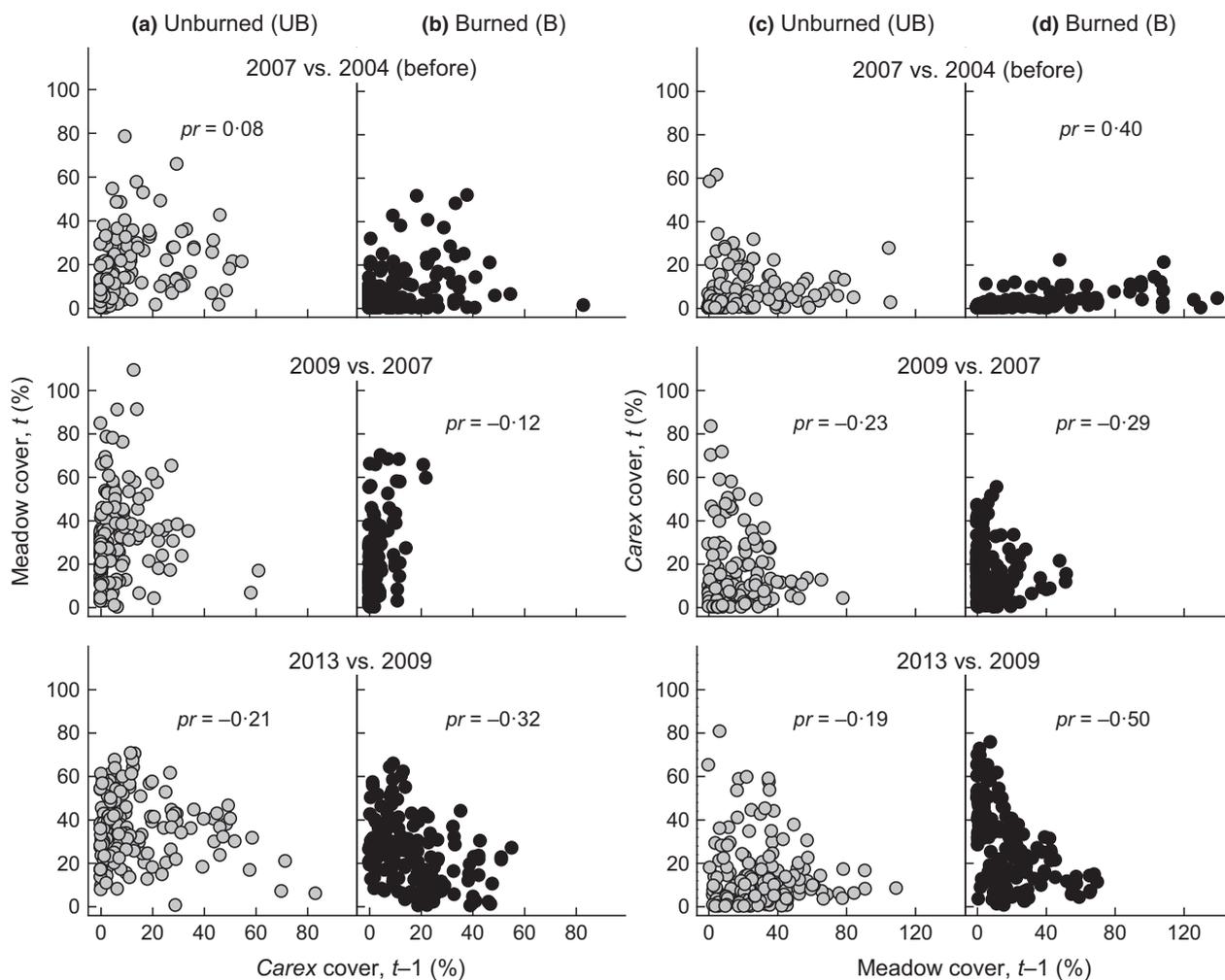
Fig. 4. Effects of previous ($t-1$) on current (t) cover of meadow species (a, b) and *Carex* (c, d) during each sampling interval. Partial correlations (pr) are shown if significant in regression models (Table 1).

The strong dependence of *Carex* on past tree influence and fire is consistent with theory and empirical observations that more intact communities, with fewer open niches, are more resistant to invasion than those altered by disturbance or other factors (Kennedy *et al.* 2002; Shea & Chesson 2002). That *Carex* does not attain similar dominance in its typical habitat illustrates that invasive behaviour – triggered by disturbance – is not limited to exotic species. Native herbaceous species can be released by disturbance in a variety of forest ecosystems (see reviews in Royo & Carson 2006; Young & Peffer 2010). Following logging, clonal expansion of *Carex pensylvanica* (closely related to *C. inops*) can effect regressive succession from pine forest to sedge meadow (Abrams & Dickmann 1982). In our system, resistance to invasion by *Carex* is conferred by meadow species that regenerate rapidly where tree influence is minimal, irrespective of fire. Where meadow species are lost to encroachment, however, fire can trigger release of *Carex*, stalling reassembly – at least in the short term. Thus, it is the long-term influence of trees, not disturbance alone, which predisposes

this system to expansion by *Carex* and the transition to a novel herbaceous state.

IMPLICATIONS FOR RESTORATION

Our experiment offers unique insight into the processes that mediate meadow reassembly following tree removal and burning. It is the only large-scale restoration experiment in mountain meadows of the western North America, and one of few, globally, that tests the dependence of reassembly on the degree to which meadows have been altered by trees (*cf.* Alford *et al.* 2012). In contrast to some systems, we saw little evidence that a shift from herbaceous to woody dominance was irreversible in these meadows: Tree seedlings have re-established only at low density (Kremer, Halpern & Antos 2014) and forest herbs, which once dominated the understorey, have declined dramatically. Nevertheless, post-treatment communities show legacies of encroachment, evident in the strong dependence of the reassembly deficit on the cumulative influence of trees. Given the absence of a seed bank for most

species, reassembly thus hinges on proximity to seed sources and effective dispersal – factors that pose barriers to grassland restoration world-wide (Poschlod *et al.* 1998; Bakker & Berendse 1999). An obvious implication of our work is that tree removal will be more effective if it occurs before seed-limited species are lost from the landscape. However, species' losses to encroachment may have a less predictable consequence: once trees are removed, highly competitive species, including natives, may usurp space, inhibiting further colonization, regardless of the availability of seeds (Clark *et al.* 2007; Myers & Harms 2011; Grman, Bassett & Brudvig 2013). Additional experiments (e.g. seed additions, *Carex* removals) are needed to elucidate the roles of seed limitation and pre-emption by *Carex* in the long-term reassembly of these meadows.

Frequent or periodic burning is responsible for the open character of many grasslands. Yet, it is not likely that fire historically played this role in mountain meadows of the Pacific Northwest (Burke 1979; Vale 1981; Boyd 1999), nor in high-elevation grasslands more generally (Weigl & Knowles 2014). That burning hindered reassembly (relative to tree removal alone) suggests that other processes may favour dominance of herbaceous over woody species (e.g. gopher disturbance, climatic controls or competition). It also suggests that restoration may depend not on the nature of disturbance, but whether it modifies abiotic or biotic environments in ways that benefit target species (MacDougall & Turkington 2007). In this sense, tree removal, which enhances light availability, may be sufficient, provided that woody fuels can be reduced by pile burning without adverse effects (as demonstrated in a companion study of burn scar recovery; Halpern, Antos & Beckman 2014). Even in systems historically maintained by burning, responses to fire can shift from positive to neutral or negative when target species are lacking or fire behaviour is intensified by uncharacteristic fuel loadings. The unexpected expansion of *Carex* in this system underscores the notion that reintroduction of fire in highly altered systems can be counterproductive (Hobbs *et al.* 2006).

In sum, our results suggest that meadow restoration will be more effective (and afford greater flexibility of fuel treatments) where conversion to forest has not proceeded fully, and where treated areas encompass or adjoin remnant meadows that serve as seed sources. By experimenting with tree removal and fire over a broad range of initial vegetation states, we have demonstrated that responses to restoration are contingent on the contexts in which treatments are applied. Knowledge of these contingencies can reduce the unpredictability of restoration outcomes, thereby enhancing the economic and ecological effectiveness of management (Grman, Bassett & Brudvig 2013).

Data accessibility

Data available from the Dryad Digital Repository: doi:10.5061/dryad.tn3vp (Halpern *et al.* 2015).

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Supporting Information

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

Fig. S1. Aerial photographs and a pre-treatment stem map of a 1-ha experimental plot at Bunchgrass Ridge.

Fig. S2. Distant and quadrat-scale comparison of a reference meadow and burned subplot.

Fig. S3. Arrangement of the six experimental plots among invaded meadows at Bunchgrass Ridge.

Fig. S4. Frequency distributions of forest understory species cover and richness before treatment and at final sampling.

Table S1. Relationships among forest age structure, tree density and basal area, and abundance of meadow species and *Carex* prior to experimental tree removal.

Appendix S1. Additional details on tree removal and fuel-reduction treatments.