

RESEARCH ARTICLE

Rates, patterns, and drivers of tree reinvasion 15 years after large-scale meadow-restoration treatments

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Tree encroachment threatens the biodiversity and ecological functioning of grasslands worldwide. Reversing effects of encroachment requires not only removing trees, but limiting subsequent invasions, which can stall grassland reassembly. We quantified rates and patterns of conifer reinvasion of mountain grasslands (meadows) in western Oregon, 7 and 15 years after experimental tree removal with or without burning. We assessed frequency (percentage of 100 m² subplots) and density of reinvading trees in six 1-ha plots as a function of burn treatment, abundance in the adjacent forest (a proxy for seed availability), and distance to or orientation of forest edges. After 15 years, frequency and density of colonists varied widely among plots (24–57% of subplots and 60–250 trees/ha, respectively), but burning had no effect on either measure. *Abies grandis*, which dominated adjacent forests, was the principal invader. Colonization by less-common *Pinus contorta* and *A. procera* was correlated with species' density and basal area in adjacent forests, suggesting that establishment was seed limited. Annualized rates of invasion were similar between early and late sampling intervals (9–10/trees/ha). Establishment was generally greater along the forested edges of plots (0–10 m) than in the core (10–50 m). Prominence of shade-tolerant *A. grandis* along northerly-facing edges suggests strong microclimatic controls on establishment. In sum, tree removal, with or without prescribed fire, is successful in reversing effects of conifer encroachment. Despite abundant seed rain, reinvasion is slow and spatially restricted. Periodic hand removal of colonizing trees, while they are small, can be done efficiently and economically.

Key words: *Abies grandis*, edge effects, meadow reassembly, mountain grasslands, *Pinus contorta*, seed dispersal, seedling establishment, treatment longevity

Implications for Practice

- Tree removal, with or without fire, can be used to restore herbaceous dominance to conifer-invaded meadows or grasslands. Although trees are likely to reinvade following these treatments, rates of establishment are low, allowing for periodic removal.
- The time and cost of subsequent removal can be reduced by designing initial treatments to minimize forest-edge influences (e.g. seed rain or canopy shading), thus limiting the density and spatial dispersion of reinvading trees.
- Removal treatments should be conducted when reinvading trees are small and sparse (before they affect the surrounding vegetation); moreover, this can be done efficiently using hand tools, thus avoiding the operational challenges and potential risks of prescribed fire.

Introduction

Woody-plant invasions threaten the ecological functioning of grasslands worldwide (Scholes & Archer 1997; Van Auken 2000; Ratajczak et al. 2012; Archer et al. 2017). Multiple factors, both extrinsic and intrinsic, contribute to grassland conversion to shrubland, woodland, or forest. Among these are

changes in climate or disturbance regime that favor the establishment, growth, or survival of woody species, thus shifting the competitive balance with herbaceous species (Scholes & Archer 1997; Miller & Halpern 1998; Coop & Givnish 2007; Van Auken 2009). Woody plants can also modify biotic or abiotic conditions (competing vegetation, soils, or microclimate) to facilitate or accelerate the invasion process (Kennedy & Sousa 2006; D'Odorico et al. 2010; Halpern et al. 2010; Ratajczak et al. 2011). The shift from herbaceous to woody dominance has profound ecological consequences—reducing habitat continuity; suppressing biodiversity; and altering the storage and cycling of carbon, water, and nutrients (Jackson et al. 2002; McCarron et al. 2003; Barger et al. 2011; Ratajczak et al. 2012).

Woody-plant removal represents a first critical step in reversing the effects of encroachment. Common methods include mechanical cutting, application of herbicides, or prescribed

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burning (Hoch et al. 2002; Lett & Knapp 2005; Scholtz et al. 2018). Although these treatments are effective in shifting dominance from woody to herbaceous species, their longevity hinges on the rates at which woody plants reestablish or grow (Heisler et al. 2003; Briggs et al. 2005; Ratajczak et al. 2014). How reestablishment and growth vary with the nature of restoration treatments or the contexts in which they are applied is not well understood. Yet, these relationships are critical to management in that they dictate the need for, or timing of, further intervention. Maintaining open conditions in some grasslands may require a change in disturbance regime (e.g. frequency of burning), although the effectiveness of these strategies may hinge on other factors, including the extent of encroachment, presence or intensity of grazing, and the mechanism by which woody plants regenerate (Heisler et al. 2003; McCarron et al. 2003; Briggs et al. 2005; Ratajczak et al. 2014).

Here, we explore long-term (15-year) patterns of conifer reinvasion of mountain grasslands (or montane meadows) in western Oregon following large-scale tree-removal and burning treatments. These historically open, grass-, sedge-, or forb-dominated habitats have experienced widespread encroachment by trees since the mid-twentieth century—a process variously attributed to changes in climate, release from domestic grazing pressure, and suppression of wildfire (Vale 1981; Miller & Halpern 1998; Hadley 1999; Weigl & Knowles 2014). Loss of meadow habitat to encroachment represents an emerging conservation concern: meadows occupy a small portion of the mountain landscape, but support a rich array of plant and insect communities (McCain et al. 2014; Jones et al. 2018). In some portions of the western Cascades, tree invasion has reduced non-forest habitat by more than 50% since 1940 (Dailey 2007; Takaoka & Swanson 2008; Rice 2009) and with it, a diversity of ecosystem functions (Haugo & Halpern 2007; Highland & Jones 2014; Jones et al. 2018; Celis et al. 2019).

Our long-term experiment at Bunchgrass Ridge tests whether large-scale tree removal—with or without fire—can reverse decades to multiple centuries of conifer influence, allowing for passive reassembly of native meadow communities. Results after 8 years indicated that tree removal promoted widespread colonization by meadow species across a range of encroachment states (decades- to century-old forests). However, burning of woody residues had adverse effects—reducing survival of some target species and promoting expansion of a highly competitive meadow sedge, thus stalling reassembly (Halpern et al. 2012, 2016, 2019). Over the same period, conifers invaded gradually at low density, irrespective of fire treatment, primarily along the forested edges of plots (Kremer et al. 2014). Whether and to what extent these open habitats remain free of tree influence hinges on seedling establishment and growth in the longer term. We address these longer-term dynamics in the current study, extending the timeline to 15 years after tree removal. We focus on two aspects of tree reinvasion that are relevant to treatment effectiveness: frequency—a measure of spatial dispersion across the experimental plots—and density—a measure of abundance or intensity of tree influence. We examine how frequency and density have changed with time, how they relate to landscape- and local-scale drivers of invasion (e.g. seed supply

and edge influence), and how they vary among species with differing functional roles (i.e. shade-tolerant, late-seral vs. shade-intolerant, early-seral conifers). We address the following questions: (Q1) Have the frequency or density of colonists increased significantly over the second posttreatment decade? (Q2) If so, have annual rates of change increased or decreased over time? (Q3) Is there evidence of a lagged response to fire? (Q4) Do species' frequency or density vary with plot-scale proxies for seed availability (species' density or basal area in the adjacent forest)? (Q5) Have early associations with forest edge persisted or do current distributions suggest greater spatial dispersion of colonists?

Methods

Study Area

Bunchgrass Ridge (BG) forms a plateau at 1,350 m elevation along the boundary between the older western Cascades (volcanic flows and pyroclastic deposits of Oligocene and Miocene origin) and younger high Cascades (quaternary shield and composite volcanoes) of Oregon (Orr et al. 1992). The climate is characterized by cool, wet winters and warm, dry summers. Average minimum and maximum temperatures are -6.6°C and -0.2°C in December and 6.5°C and 22.1°C in August. Annual precipitation averages 2,290 mm, with only 14% falling from June through September resulting in frequent summer drought (WRCC 1981–2010). Most precipitation falls as snow and snowpack can persist into May or early June.

The study area supports a mosaic of open grasslands (or meadows) and forests of varying age and structure, reflecting two centuries of conifer encroachment (Fig. 1; Halpern et al. 2010; Rice et al. 2012). Meadows comprise diverse communities of graminoids and forbs characteristic of mesic and dry habitats of this region (McCain et al. 2014). Forests are dominated by *Abies grandis*; less abundant species include *Pinus contorta* var. *latifolia* (lodgepole pine), *Pseudotsuga menziesii* var. *menziesii* (Douglas-fir), and *A. procera* (noble fir) (Table 1). Nomenclature follows Meyers et al. (2015).

Soils at BG are deep (1.7 m), fine to very fine sandy loams derived from andesitic basalt and tephra deposits with varying amounts of glacially derived rock. Soil profiles indicate dominance of grassland vegetation for centuries (possibly millennia), even in areas that currently support forest (D. Lammers 2004, personal communication). They grade from Vitric Melanocryands (open meadows) to Aquic Vitricryands (older forests). Soil biogeochemical properties have been described previously (Griffiths et al. 2005).

The factors responsible for recent tree invasion at BG remain unclear. Trees established at low density during the late 1800s, but in greater abundance after 1950 (Halpern et al. 2010; Rice et al. 2012), reducing the area of open meadow by more than 50% (Rice 2009). The timing of recent invasion was correlated only weakly with variation in climate (Halpern et al. 2010; Rice et al. 2012). Although establishment may have been triggered by cessation of sheep grazing in the early to mid-1900s (Elliot 1946; Burke 1979; Johnson 1985)—as documented



Figure 1. Distribution of the six 1-ha experimental plots at Bunchgrass Ridge. Following tree removal in Jan–Feb 2006, woody residues were broadcast burned (red numbered plots) or pile-burned, leaving 90% of the ground surface unburned (black numbered plots). Upper left and right photos illustrate invasion of plot 2 by *Pinus contorta* and plot 3 by *Abies grandis*, respectively (photos by C. Halpern).

elsewhere in the Cascades and Sierra Nevada (Vale 1981; Ratliff 1985; Taylor 1990; Miller & Halpern 1998)— there are no records of grazing history at BG in Forest Service archives. Recent invasion could reflect a reduction in fire frequency,

although at this elevation, natural ignitions are infrequent (Morrison & Swanson 1990; Weisberg & Swanson 2003; Tepley et al. 2013). Anthropogenic burning occurred historically in the broader landscape (Burke 1979; Boyd 1999), but

Table 1. Density, basal area, and height of the principal tree species in forests adjacent to each plot in 2013 (from Kremer et al. 2014). Data are for trees ≥ 10 cm dbh in a 20-m-wide band surrounding each plot (occasionally 30 m wide where tree density was low). Height was estimated from diameter (dbh) based on dbh-height relationships (C. Halpern unpublished data).

Plot	Abies grandis			Pinus contorta			Pseudotsuga menziesii			Abies procera		
	Density (trees/ha)	Basal area (m ² /ha)	Mean height (m)	Density (trees/ha)	Basal area (m ² /ha)	Mean height (m)	Density (trees/ha)	Basal area (m ² /ha)	Mean height (m)	Density (trees/ha)	Basal area (m ² /ha)	Mean height (m)
2	233.8	8.8	17.4	37.5	1.5	21.6	37.5	2.0	18.4	2.5	0.0	12.4
3	164.2	8.7	17.9	21.3	0.7	21.3	6.3	0.7	22.2	1.3	0.0	8.9
8	172.5	24.3	22.1	1.3	<0.1	18.3	3.8	1.4	28.1	8.8	0.4	19.4
10	391.3	38.3	20.9	12.5	0.7	24.9	5.0	0.4	20.5	20.0	1.3	20.5
11	117.5	11.8	20.5	0.8	0.3	22.6	11.7	1.8	23.9	5.8	0.6	24.1
13	363.8	23.9	19.0	17.5	0.8	22.5	12.5	6.3	27.3	0.0	0.0	—

archeological surveys of BG have failed to produce artifacts of human use (Haugo & Halpern 2007) and there is no evidence of more frequent fire in the past. Despite uncertainty about past disturbance, spatiotemporal reconstructions at BG point to strong biotic controls on the invasion process, with initial recruits facilitating subsequent establishment (Halpern et al. 2010; Rice et al. 2012).

In 1990, BG was designated as Special Habitat Area in the Willamette National Forest Land and Resource Management Plan. In 1995, it was targeted as a priority area for restoration as part of the Upper McKenzie Watershed Analysis, with the objectives of enhancing wildlife habitat (forage quantity and quality), restoring native grassland/meadow, and reducing fuel loadings. The current experiment, initiated in 2003, was designed to test the efficacy of tree removal—with or without fire—in achieving these objectives (Halpern et al. 2012, 2014, 2016, 2019).

Experimental Design and Sampling

We used historical aerial photographs and field reconnaissance to delineate a 16-ha area of tree-invaded meadows for experimentation. Within this area we established nine 1-ha (100 × 100 m) plots (Fig. 1), each containing a fine-scale mosaic of meadow openings and forests of varying age and structure (Haugo & Halpern 2007; Halpern et al. 2010). Plots were assigned randomly to one of three treatments: (1) control: no trees removed; (2) burned: all trees removed and slash broadcast burned; or (3) unburned: all trees removed and residual slash piled and burned leaving 90% of the ground surface unburned. Here, we consider only the tree-removal plots. To minimize ground disturbance, trees were cut and yarded on deep snow in Jan–Feb 2006. Broadcast burning occurred on 28 September 2006. In burned plots, fine (1- to 100-hour) fuels, which averaged 53 to 69 Mg/ha, burned to completion within 2 hours. Flame lengths averaged 1 to 2 m and fine-fuel consumption averaged 67 to 87%. Cover of burned ground (charred litter or white ash) varied spatially within plots, ranging from 0 to 99% (plot means of 63 to 77%); cover of bare soil ranged from 0 to 71% (plot means of 15 to 19%) (Halpern et al. 2012). Slash piles in the unburned plots were lit on 2 November 2006 and burned to completion (95 to 100% consumption) within 2 days. For additional details see Halpern et al. (2012, 2014).

In 2003 (prior to tree removal) we established a permanent grid in each plot, creating a contiguous array of one hundred 10 × 10-m subplots. Data for the current study were collected in 2013 and 2020 (8 and 15 years after tree removal). In 2013, all trees ≥ 5 cm tall were tallied by subplot, measured for height, and aged to distinguish colonists from residuals (trees surviving disturbance; Kremer et al. 2014). In 2020, tallies and height measurements were repeated in each subplot for trees at least 20 cm tall.

Statistical Analyses

Data were reduced prior to analysis to achieve comparability between sampling dates. Seedlings less than 20 cm tall (not

sampled in 2020) were dropped from the 2013 data. Residuals were removed from the 2020 data based on subplot-scale counts made in 2013. Removal of residuals reflects two assumptions. First, it assumes that residuals shorter than 20 cm in 2013 were taller than 20 cm in 2020 (consistent with reconstructed growth rates of 7 cm/year; Kremer et al. 2014). Second, it assumes that residuals present in 2013 survived to 2020. Mortality and age data from 2013 support this assumption: dead stems comprised fewer than 4% of total stems and most were colonists (Kremer et al. 2014).

For each plot, we used subplot-scale data to generate “bubble plots” displaying the spatial distributions and densities of tree species in 2020. Statistical analyses focused on two aspects of colonization: frequency (percentage of subplots, a measure of spatial dispersion) and mean density (trees/ha, a measure of abundance). To assess changes in frequency or density among plots between 2013 and 2020 (Q1), we used a series of paired *t* tests ($n = 6$ plots) or, where necessary, the nonparametric Wilcoxon-signed-rank test. Separate tests were run for conifers as a group and for each of the primary species (*Abies grandis*, *Pinus contorta*, *Pseudotsuga menziesii*, and *A. procera*).

To determine whether the pace of invasion changed between early (2006–2013) and late (2013–2020) sampling intervals (Q2), we computed a “net invasion rate” for each interval, expressing the annualized change in density due to colonization and mortality. Net invasion rates were estimated for plots as whole and for “edge” and “core” subplots within each plot (see definitions below). Estimates for the early interval accounted for the differing times since disturbance in burned versus unburned plots (7 vs. 8 years). Separate paired *t* tests ($n = 6$ plots) or Wilcoxon-signed-rank tests were run for conifers as a group and for each of the primary species. To test for lagged responses to fire (Q3), we compared frequency or density between burned and unburned plots using Welch two-sample *t* tests or Mann–Whitney *U* tests ($n = 3$ plots per treatment).

To determine whether colonization metrics correlated with abundance of trees in the adjacent forest—a proxy for seed availability (Q4)—we computed, for each species, a set of Spearman rank correlations between frequency or density of seedlings, and density or basal area of trees within 20 m of the plot (occasionally 30 m where tree density was low; Kremer et al. 2014). Density and basal area were based on trees at least 10 cm in diameter at breast height (dbh), that is, those likely to be reproductive.

In addition to these plot-scale metrics, we tested whether early associations with forest edge persisted into the late sampling interval (Q5). Specifically, for each species (and for conifers as a group) we compared frequency and density for subplots representing (1) increasing distances from the forest edge (i.e. 0–10, 10–20, 20–30, and 30–50 m) and (2) northerly (NW to NE) versus southerly (SW to SE) facing edges (0–10 m). Preliminary analyses showed little change in frequency or density beyond 10 m, thus we simplified the distance comparisons to subplots representing “edge” versus “core” environments, that is, 0–10 versus 10–50 m ($n = 36$ and 64 subplots per plot, respectively; for exceptions see Fig. 2). As with previous analyses, we used paired *t* tests or Wilcoxon-signed-

rank tests, as appropriate ($n = 6$ plots). Analyses were conducted with JMP Pro 15.2.0 (SAS 2019).

Results

In 2020, 15 years after tree removal, we tallied a total of 827 colonizing trees (≥ 20 cm tall) in the six 1-ha plots. Seven years

earlier (2013), the total was 454. *Abies grandis* remained the most common species—543 trees in 2020 versus 361 in 2013—but its relative abundance declined from 80 to 66% of the total. *Pinus contorta* and *A. procera* were less common, but increased proportionally more in number: from 34 to 134 and from 8 to 70, respectively. *Pseudotsuga menziesii* invaded more slowly, increasing in number from 49 to 68. In

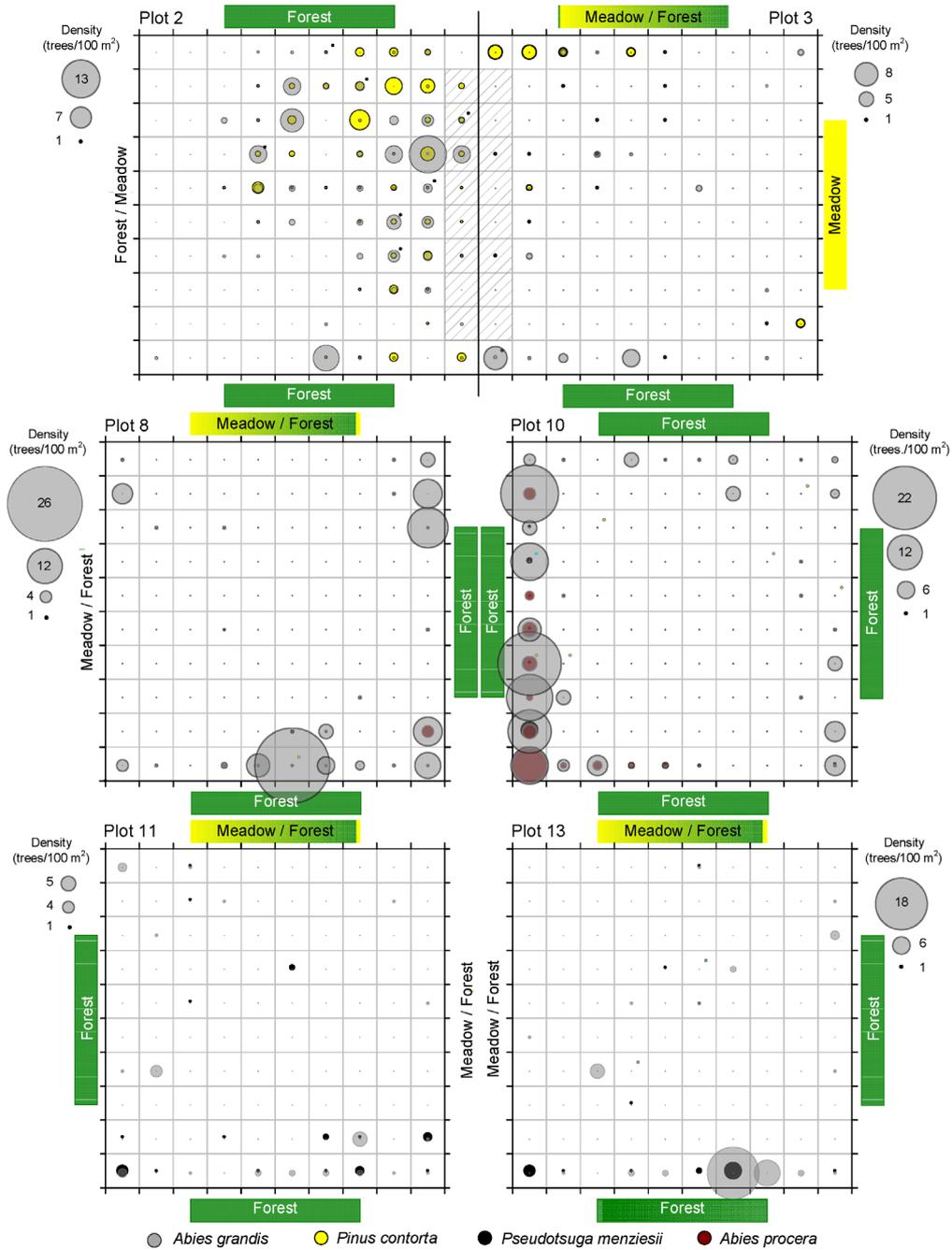


Figure 2. Density distributions of invading trees (≥ 20 cm tall) in each plot in 2020. Circle size is proportional to density within a subplot (100 m^2). Species are coded by color. In plots 10 and 13, single individuals of *Pinus monticola* and *Tsuga heterophylla* are not shown. Colored bars indicate whether plots are bordered by forest (green), meadow (yellow), or both (see Fig. 1). The forest edge at the bottom of each plot is northerly facing (NW to NE). Plots 2 and 3 share an east-west edge; subplots with gray hatching were dropped from “edge” versus “core” comparisons.

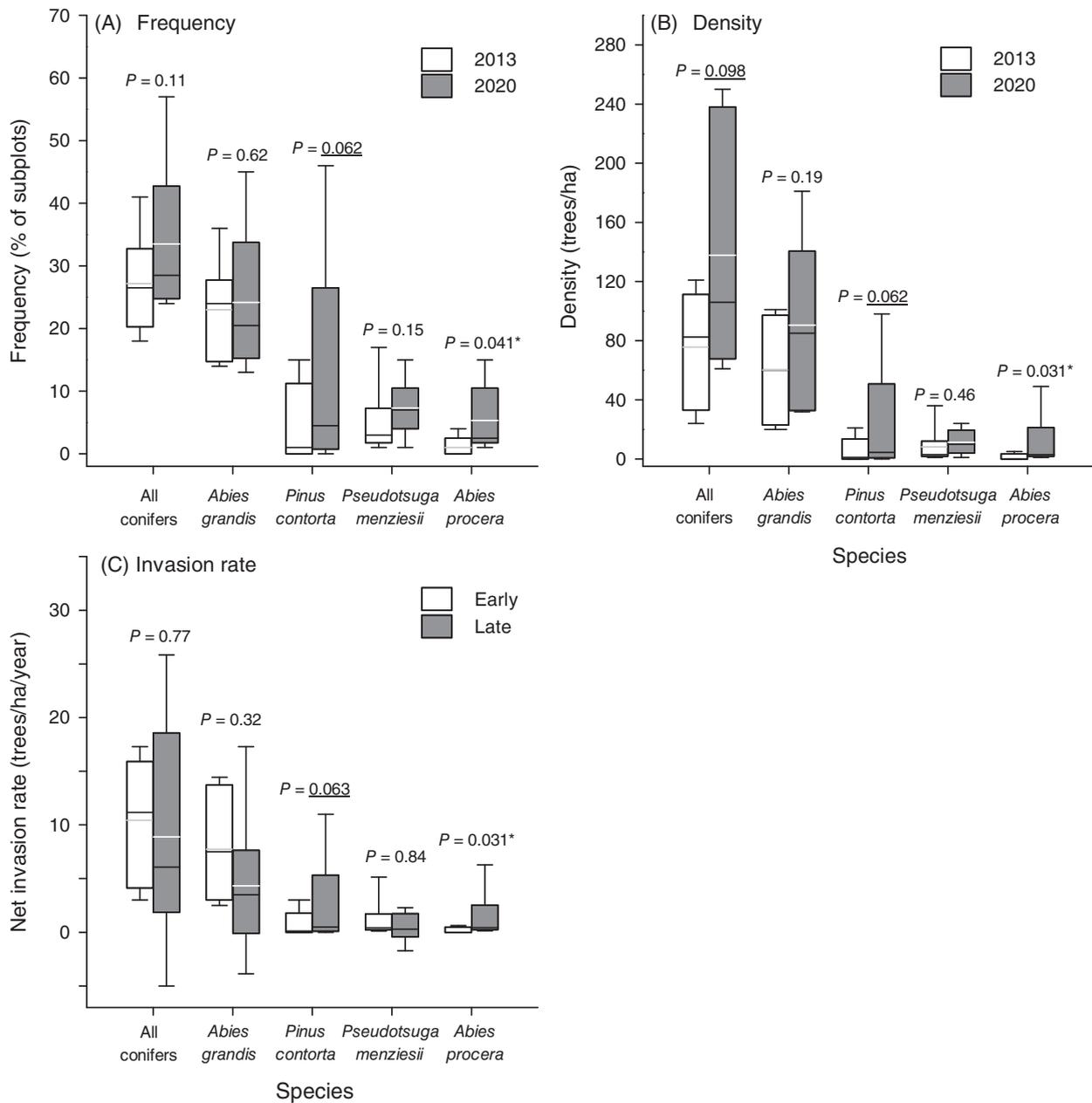


Figure 3. (A) Frequency and (B) density of invading trees (≥ 20 cm tall) in 2013 versus 2020 and (C) net invasion rate (annualized change in density) in the early (2006–2013) versus late (2013–2020) sampling intervals. Values are the median (black line), mean (gray or white line), interquartile range, and range ($n = 6$ plots). A negative net invasion rate in the late sampling interval indicates a decline in density. p -Values are from paired t tests (if means are shown) or Wilcoxon signed-rank tests comparing sampling dates or intervals. Asterisk (*) indicates statistical significance ($p \leq 0.05$); underscore indicates marginal significance ($0.05 < p \leq 0.10$).

2020, the median tree height was 0.4 m for both *Abies* species, but more than twice that for *P. contorta* (1.0 m) and *P. menziesii* (1.4 m). Maximum heights ranged from 2.4 m in *A. procera* to 4.5 m in *P. menziesii*.

Changes in Frequency, Density, and Net Invasion Rate (Q1, Q2)

The frequency, density, and composition of colonists varied widely among plots (Fig. 2). Frequency of conifers, as a

group, did not increase significantly between 2013 and 2020; plot values ranged from 18 to 41% and from 24 to 57%, respectively (Fig. 3A). Density, however, showed a marginally significant increase, with plot values ranging from 24 to 121 trees/ha in 2013 and from 61 to 250 trees/ha in 2020 (Fig. 3B). *Abies grandis*, the principal colonist, showed little change in frequency and density, but *A. procera* and *P. contorta* increased significantly or marginally so (Fig. 3A & 3B).

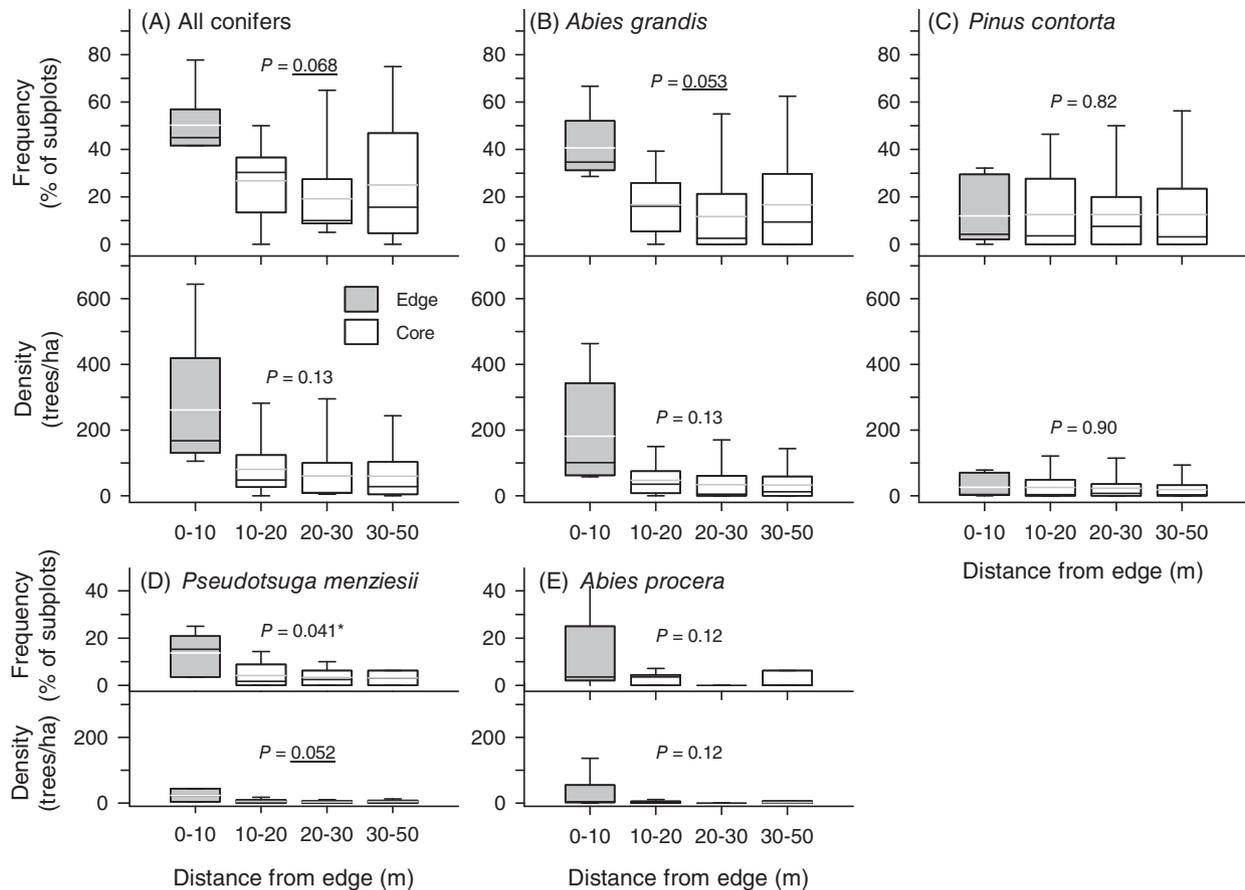


Figure 4. Frequency and density of invading trees (≥ 20 cm tall) as a function of distance from plot edge for (A) conifers as a group and (B–E) each of the primary species. The 0–10 m bin (gray bar) represents the “edge” environment. The remaining three bins (white bars) represent concentric rings of subplots at increasing distance from edge; in combination (10–50 m), they constitute the “core” environment. *p*-Values are from paired *t* tests (if means are shown) or Wilcoxon-signed-rank tests comparing “edge” versus “core” subplots. See Figure 3 for other details.

Net invasion rates (annualized changes in density) did not change significantly between the early and late intervals for conifers as a group, or for *A. grandis* (Fig. 3C). Plot-scale values for *A. grandis* ranged from 2.5 to 14.4 trees ha⁻¹ year⁻¹ in the early interval and from -3.9 to 17.3 trees ha⁻¹ year⁻¹ in the late interval. In contrast, net invasion rates increased significantly between early and late intervals for *A. procera* (plot ranges of 0.0 to 0.6 trees ha⁻¹ year⁻¹ vs. 0.1 to 6.3 trees ha⁻¹ year⁻¹, respectively), and increased marginally for *P. contorta* (plot ranges of 0.0 to 3.0 trees ha⁻¹ year⁻¹ vs. 0.0 to 11.0 trees ha⁻¹ year⁻¹, respectively) (Fig. 3C).

Relationships to Fire (Q3) and Seed Supply (Q4)

Species’ frequency and density did not differ between burned and unburned treatments (*p* > 0.42 for all comparisons), consistent with early responses to fire.

Relationships between colonization frequency or density and tree density or basal area in the adjacent forest (proxies for seed availability) varied in strength among species (Table S1). Correlations were considerably stronger for *A. procera* (*rho*: 0.89 to 0.99) and *P. contorta* (*rho*: 0.75 to

0.94) than for the dominant, *A. grandis* (*rho*: 0.37 to 0.77), or *P. menziesii* (*rho*: 0.37 to 0.55) (Table S1).

Associations With Forest Edge and Edge Orientation (Q5)

For conifers as group, frequency of colonization was marginally greater in edge (0–10 m) than in core subplots (10–50 m) (Fig. 4A), consistent with the pattern in 2013 (Kremer et al. 2014). Among the six plots, frequencies ranged from 39 to 78% of edge subplots and from 12 to 61% of core subplots. Although the corresponding densities trended higher at the edge (106 to 644 trees/ha) than in the core (20 to 276 trees/ha), means did not differ statistically (Fig. 4A). *Abies grandis* was more numerous (Fig. 4B) but *P. menziesii* showed stronger associations with edge (Fig. 4D). *Pinus contorta* was distinct in showing no evidence of an association with edge (Fig. 4C).

For most species, net invasion rates did not change between early and late sampling intervals in either edge or core environments (Fig. 5). There were two exceptions, however: *A. procera* had a marginally significant increase in median rate at the edge (0.0 to 0.5 trees ha⁻¹ year⁻¹, respectively; Fig. 5A) and

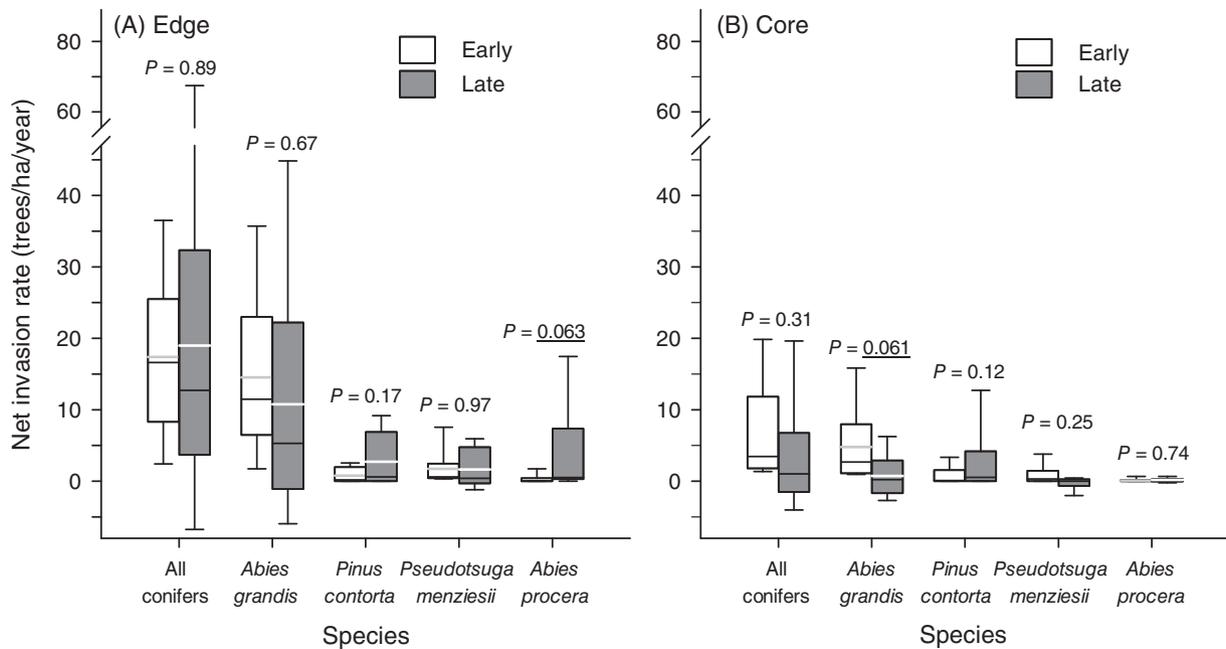


Figure 5. Net invasion rates (annualized change in tree density) in (A) edge and (B) core subplots during the early (2006–2013) and late (2013–2020) sampling intervals. A negative value in the late interval indicates a decline in density. See Figure 3 for other details.

A. grandis had a marginally significant decline in mean rate in the core (4.8 to 0.7 trees ha⁻¹ year⁻¹, respectively; Fig. 5B).

Orientation of the forest edge had strong effects on colonization (Fig. 6). *Abies grandis* showed a distinct association with northerly (N-) facing edges, as did *P. menziesii*. For *A. grandis*, density consistently exceeded 130 trees/ha

and ranged as high as 600 trees/ha on N-facing edges. In contrast, along S-facing edges it rarely exceeded 70 trees/ha and peaked at 160 trees/ha (Fig. 6B). Edge orientation did not have a significant effect on *P. contorta*, but its peak frequency and density occurred along S-facing edges (Figs. 2 & 6).

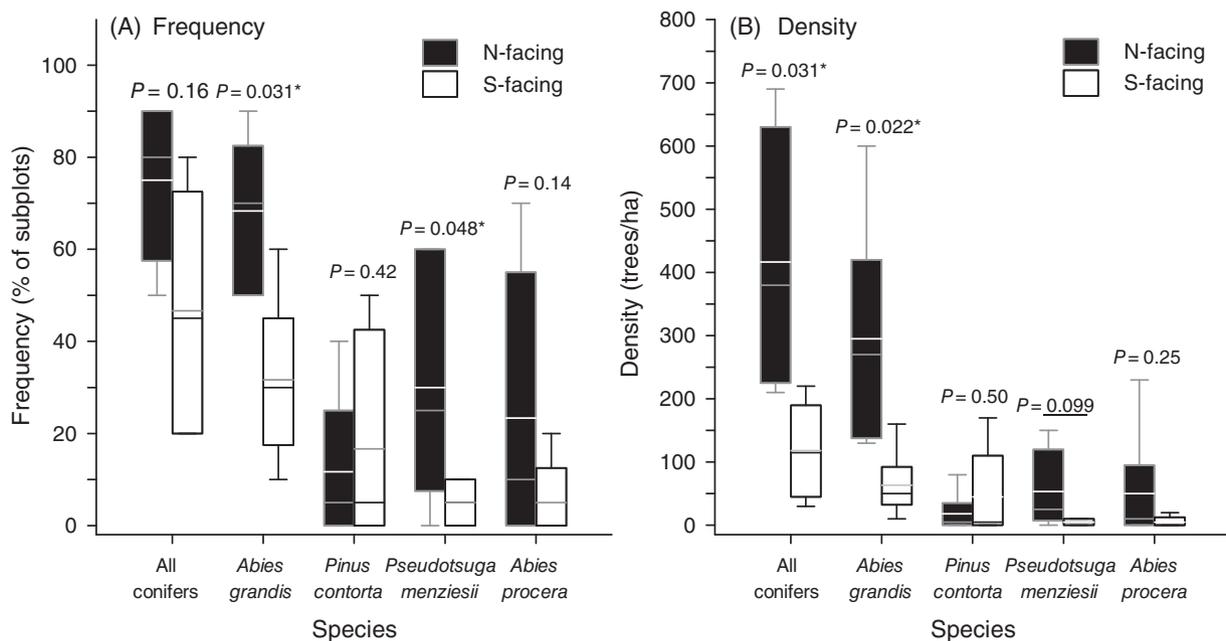


Figure 6. (A) Frequency and (B) density of invading trees (≥ 20 cm tall) in subplots representing northerly (N-) and southerly (S-) facing forest edges (0–10 m). See Figure 3 for other details.

Discussion

Tree removal represents a first critical step in restoring the structure and functioning of conifer-invaded mountain meadows. Although many factors can affect their recovery, tree reinvasion poses an obvious challenge. If allowed to grow, tree seedlings can outcompete resident meadow species (Haugo & Halpern 2010) and create new foci for further recruitment, clump expansion, or dispersal (Archer et al. 1988; Duarte et al. 2006; Boulant et al. 2008; Halpern et al. 2010). Indeed, reconstructions of twentieth-century encroachment at BG suggest that meadows were replaced by forests within four decades of establishment, as tree densities exceeded 4,000 stems/ha (Haugo & Halpern 2007; Rice et al. 2012). Results of the current study suggest a considerably slower, but spatially variable process of reinvasion.

Results of our 15-year study underscore the efficacy of tree removal, with or without fire, in limiting conifer reinvasion during meadow reassembly. In a system characterized by infrequent fire, prescribed burning neither promoted nor reduced tree establishment. Although bare soil was exposed, providing seedbed conditions that favor conifer germination (Kilgore 1973; Zald et al. 2008; Schwilk et al. 2009), the effect was transient (Halpern et al. 2012) and overshadowed by the more pervasive, soil-disturbing activities of gophers (Jones et al. 2008; Case et al. 2013).

Despite a near doubling of seedling numbers between 2013 and 2020, we did not see a consistent increase in frequency (spatial dispersion of colonists). In fact, with the exception of plot 2, the vast majority (62–76%) of subplots remained free of trees. Trends in net invasion rate—expressing change in density on an annual basis—paint a similar picture of subtle change in time but marked variation in space. Although the net invasion rate averaged 9–10 trees ha⁻¹ year⁻¹ in both the early and late sampling intervals, it varied widely among plots—from negative (–5 trees ha⁻¹ year⁻¹, where mortality exceeded colonization) to strongly positive (26 trees ha⁻¹ year⁻¹). We attribute this spatial variability to variation in “forest influence” (sensu Baker et al. 2013; Baker et al. 2014) manifested in the seed rain (Clark et al. 1999; Dovčiak et al. 2008), effects of canopy shading (Heithecker & Halpern 2007; Baker et al. 2014), or belowground interactions (mycorrhizal associations; Dickie & Reich 2005; Outerbridge & Trofymow 2009). Colonization was greatest in plot 10—fully surrounded by forest—but notably lower in plots 3, 11, and 13, where forests were absent or more distant from one or more edges. This variation in the frequency or density of colonization highlights the importance of propagule pressure in driving reinvasion. It also has implications for the layout, or spatial structure, of future restoration treatments: edge influences can be reduced if treated areas are separated—even by short distances—from residual forests. Targeting tree removal to the margins of existing meadows or expanding smaller openings should be more effective than creating new edges or openings.

We also observed variation in the timing, density, and spatial distribution of recruitment among species, suggesting differing controls on invasion. For shade-tolerant *A. grandis*, which dominated the landscape, plot-scale frequency and density were correlated weakly with abundance in the adjacent forest, suggesting

that establishment was not seed limited. Rather, establishment appeared constrained by microsite (environmental) conditions, resulting in a strong association with N-facing edges and a temporal decline in colonization of the core. In contrast, for *P. contorta* and *A. procera*—species with sparser distributions in the landscape—spatiotemporal patterns of invasion suggest that seed was limiting. Previously (2013), neither species had established in a sufficient number of plots to be able to assess relationships with seed availability (Kremer et al. 2014). By 2020, however, plot-scale frequency and density had increased 4- to 9-fold, and were highly correlated with abundance in the adjacent forest.

These contrasts in the timing, spatial patterning, and drivers of establishment highlight an important result of this experiment—that species’ roles in the invasion process can change with the seral state of the surrounding forest. Although *P. contorta* was major contributor to nineteenth- and twentieth-century invasions at BG (Halpern et al. 2010; Rice et al. 2012), it has played a relatively minor role posttreatment due to its decline in the landscape. Several factors have contributed to this decline: intolerance of shade (Minore 1979), a shorter lifespan than late-seral *A. grandis* (Lotan & Critchfield 1990), and recent losses to beetle-kill, possibly related to summer drought. Had treatments been imposed during an earlier stage of encroachment, *P. contorta* would likely have played a larger role, establishing more broadly and creating new foci for recruitment and dispersal (Archer et al. 1988; Boulant et al. 2008; Halpern et al. 2010).

Current patterns of colonization suggest that edge environments remain more conducive to establishment than areas more distant from edge influence (Kremer et al. 2014). Frequency and density declined sharply beyond 10 m for *A. grandis* and *P. menziesii*, although for *A. grandis* density, plot-to-plot variation in the core precluded detection of a significant edge effect. Temporal trends in net invasion rate paint a slightly different picture of this dynamic. For *A. grandis*, the net invasion rate did not increase at the edge, suggesting that densities were too low (or trees were too small) to initiate positive interactions or feedbacks (Duarte et al. 2006; Halpern et al. 2010; Rice et al. 2012). In contrast, the invasion rate declined in the core, suggesting that safe sites for regeneration were being saturated (Dovčiak et al. 2008). Moreover, in some plots, mortality exceeded recruitment, resulting in a decline in density. Smaller seedlings may be susceptible to herbivory or physiological stress in the open, including root pruning or girdling by northern pocket gophers (Burton & Black 1978; Teipner et al. 1983), browsing by elk (Graham & Kingery 1990; Jenkins & Starkey 1993), summer drought (Foiles et al. 1990), and root competition with the highly clonal native sedge, *Carex inops* (Halpern et al. 2016). Surviving the joint effects of physical damage and stress may be a particular challenge for slow-growing, shade-tolerant species such as *A. grandis*.

It is difficult to infer mechanisms of association with forest edge from the spatial distributions of seedlings: seed rain, canopy shading, and mycorrhizal abundance form complex, covarying gradients with distance from edge. In this study,

edge-related declines in colonization were consistent with the spatial scales over which these gradients manifest. For example, in studies of seed dispersal into harvest units, density of seed rain for *Abies* species declined by 66 to 75% within 40 m of the edge (Franklin & Smith 1974; Carkin et al. 1978). Strong associations with forest edge are also consistent with the short distances (5 to 10 m) over which the roots of edge trees promote ectomycorrhizal colonization of tree seedlings (Dickie & Reich 2005; Outerbridge & Trofymow 2009). Finally, for late-seral *A. grandis*, which typically regenerates in the shade (Foiles et al. 1990), the strong association with N-facing edges suggests microclimatic control of establishment (Chen et al. 1995; Heithecker & Halpern 2007; Baker et al. 2014). Although canopy shading can extend as far as 40 m from the edge (for trees of comparable height), light levels decline rapidly in the first 5–10 m (Heithecker & Halpern 2007; Celis et al. 2019). In contrast to *A. grandis*, the association of early-seral *P. menziesii* with N-facing edges is not as easily explained by microclimatic variation. Although first-year survival is enhanced by partial shade (Isaac 1943; Hermann & Lavender 1990), growth is best under full sun (Minore 1979; Carter & Klinka 1992; Maily & Kimmins 1997). We suspect that the pattern is driven, in part, by variation in seed supply: *P. menziesii* was patchily distributed across the BG landscape and some of the largest stems were found along the southern boundaries of plots 11 and 13. In sum, propagule pressure appears to drive the reinvasion process for multiple species at a range of spatial scales, although edge-related gradients in the environment can mediate the effectiveness of the seed rain (Rouget & Richardson 2003; Dovčiak et al. 2008; Pauchard et al. 2016).

Collectively, the small stature and sparse, nonaccelerating rates of establishment imply that large areas of meadow remain free of tree influence, even after 15 years. At current densities and rates of growth, it may take an additional decade or more for established trees to affect the surrounding vegetation. Thereafter, change can be rapid, particularly under the denser canopy of *A. grandis* (Haugo & Halpern 2010). Removing trees manually, while they are small, can be accomplished effectively at minimal cost. At BG, it took little more than a day for a crew of six using hand tools (loppers and saws) to cut and scatter the more than 800 trees sampled. Although prescribed fire can also be used to kill newly established tree seedlings, in this system it can have adverse effects—reducing survival or slowing recolonization of meadow specialists (Halpern et al. 2016, 2019). Given the pace of recruitment and slow growth of shade-tolerant *A. grandis*, a 20-year maintenance schedule for removal may be sufficient. Faster-growing conifers such as *P. contorta* or *P. menziesii* could be targeted more frequently, although in this system their densities were, and are likely to remain, quite low. The greater challenge to meadow restoration lies in implementing initial and re-entry treatments at a landscape scale, as operational and economic costs are weighed against other resource management and conservation priorities.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Spearman rank correlations between frequency or density of colonists in the experimental plots and density or basal area of trees in the adjacent forest.

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