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ORIGINAL PAPER

The importance of disturbance by fire and other abiotic and biotic factors in driving cheatgrass invasion varies based on invasion stage

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Abstract Disturbances create fluctuations in resource availability that alter abiotic and biotic constraints. Exotic invader response may be due to multiple factors related to disturbance regimes and complex interactions between other small- and large-scale abiotic and biotic processes that may vary across invasion stages. We explore how cheatgrass responds to both frequency and season of prescribed burning for a 10-year period in ponderosa pine forested stands. To understand interactions of fire disturbance, other abiotic factors, biotic resistance, and propagule pressure, we use long-term data from different spatial scales representing different invasion stages (local establishment or spread and broader scale extent/impact) to model cheatgrass dynamics. We found that after 10 years, cheatgrass cover increased with fall burning regardless of burn frequency (1 burn vs. 3 burns). There was no evidence that cheatgrass invasion is decreasing through time even in areas burned only once. Factors important for explaining local fine-scale cheatgrass establishment and spread, and broader scale extent/impact varied. The spatial extent of the first burns facilitated fine-scale cheatgrass establishment while bare soil cover constrained establishment. Biotic resistance, in the form of native annual forb cover, constrained fine-scale cheatgrass spread. Initial cheatgrass abundance in 2002, a factor related to propagule pressure, was key for explaining the broader scale extent/impact of cheatgrass by 2012. Biotic resistance, in the form of native perennial grass cover, constrained extent/impact but only when initial cheatgrass abundance was low. Our findings regarding factors affecting invasion dynamics may be useful to consider for future restoration and conservation efforts in burned ponderosa pine forests.

Keywords Propagule pressure · Cheatgrass · *Bromus tectorum* · Prescribed fire · Burn interval

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Introduction

Reintroducing fire as an important historical disturbance regime is considered critical for the restoration of many fire-dependent coniferous ecosystems in North America (Covington 2000). However, desired restoration outcomes can be hindered by the introduction and spread of exotic invasive species (D'Antonio

and Meyerson 2002) especially after fire (D'Antonio 2000). Disturbances such as extreme climatic events (e.g., floods, droughts) and fire can create fluctuations in resource availability through abiotic (soil N, light availability) and biotic (aboveground biomass, diversity) mechanisms and alter abiotic and biotic constraints leading to invader dominance (Davis et al. 2000; Collinge et al. 2011; Byun et al. 2015). In forests, disturbances such as fire remove litter accumulation, reduce aboveground biomass, and often open up forest canopies allowing exotic invaders to increase in abundance (Knapp and Seastedt 1986; Kerns et al. 2006). However, fire does not always lead to increases in invaders, or increases may be ephemeral as native species recover and compete for resources (e.g., Wein et al. 1992; D'Antonio 2000; Bates et al. 2005). Divergent responses of an exotic invasive species to fire may be due to multiple factors related to burn timing, frequency and season; variability in fire intensity; and burn extent and subsequent severity (e.g., litter removal, perennial native species mortality). Repeat burning has been shown to reduce the abundance and dominance of some exotic grasses (Svedarsky et al. 1986; Parsons and Stohlgren 1989; Menke 1992; Smith and Knapp 1999, 2001) although in many ecosystems with exotic annual grass populations, can lead to invader dominance, a phenomenon that has been documented globally (D'Antonio and Vitousek 1992).

Divergent responses of an exotic invasive species to disturbance may also be due to complex interactions and feedbacks between disturbance regimes and other small- and large-scale abiotic and biotic processes. Biological invasions initiate complicated community reassembly processes, and outcomes hinge on multiple interacting factors (Levine et al. 2004; Dietz and Edwards 2006; Catford et al. 2009; Byun et al. 2015). For example, hypotheses regarding invasion success and impact are often structured in the context of the long-held theory that species rich communities should be less susceptible to invasion (Elton 1958; Levine and D'Antonio 1999). But empirical support for this idea has been mixed with studies documenting both negative and positive effects of diversity on invasibility (Levine and D'Antonio 1999; Stohlgren et al. 1999a; Dukes 2002; Questad et al. 2012), with results that often depend on scale (Fridley et al. 2007) or disturbance (Pinto and Ortega 2016). Although studies have examined interactions between abiotic and biotic factors (e.g., Hobbs and Huenneke 1992; Levine and D'Antonio 1999), complex interactions between disturbance, other abiotic factors, biotic processes, propagule pressure and invasion are rarely studied together (Lowry et al. 2013) (but see Eschtruth and Battles 2009), and we know of no studies that incorporate disturbance regimes. The interplay among these factors may also change across invasion stages from establishment to spread and ultimately to impact. For example, exotic propagule pressure can modulate the effectiveness of biotic resistance during the colonization stage of invasion (Byun et al. 2015), but prove insufficient to overcome biotic resistance in already invaded areas (McGlone et al. 2011). Long-term data are required to address changes across multiple stages and only a handful of studies have examined long-term patterns of invasion and interactions between multiple factors (e.g., Wiser et al. 1998; Collinge et al. 2011; McGlone et al. 2011). The relative importance of both abiotic and biotic factors also depends on scale. Thus multiscale investigations can provide important insights (e.g., Pauchard and Shea 2006).

We use long-term data to investigate the dynamics of cheatgrass (*Bromus tectorum*) invasion under varying biotic and abiotic conditions across a range of sites and through various stages of invasion in ponderosa pine forests disturbed by prescribed fire. Cheatgrass is an exotic annual grass linked to numerous negative impacts because it has the potential to drastically disrupt multiple ecosystem processes (D'Antonio and Vitousek 1992) and is considered an ecosystem "transformer" (sensu Richardson et al. 2000). We measured forest understory vegetation response to both frequency and season of prescribed burning (spring, fall or no burning repeated every 5 years vs. a single burn) for a 10-year period (Kerns et al. 2006). We address two questions regarding cheatgrass invasion success. First, what is the effect of disturbance regime characteristics (season and frequency) on cheatgrass cover? Second, how are patterns in local and fine-scale cheatgrass establishment, spread, and broader scale extent/impact potentially facilitated or constrained by disturbance regime, other abiotic factors, biotic resistance, and propagule pressure? We use three sets of data from two spatial scales that represent different processes or "stages" of invasion. Our invasion stage names are derived from the literature (Levine et al. 2004; Colautti et al. 2006;

Catford et al. 2009; Eschtruth and Battles 2011) but we note that invasion "stages" are not necessarily linear nor discrete events, but rather long-term processes that operate within a dynamic ecological context (Dietz and Edwards 2006). We use the term extent/impact in acknowledgement of the fact that we did not directly measure impact (Jeschke et al. 2014), but recognizing that there is a link between cheatgrass extent and development of the highly impactful grass-fire cycle (D'Antonio and Vitousek 1992; Balch et al. 2013).

Methods

Study area

The study was conducted using five upland forested stands that span a productivity gradient located at the southern end of the Blue Mountains within the Malheur National Forest, Oregon (Kerns et al. 2006). The stands are dominated by mixed-aged ponderosa pine, but *Juniperus occidentalis* and *Cercocarpus ledifolius* also occur. Differences in understory floristic composition among the stands were apparent (Kerns et al. 2006). The lower site productivity eastern area stands have lower overall plant cover, and more xeric type vegetation than the two western stands (understory dominated by bunchgrasses such as *Pseudoroegneria spicata* and *Elymus elymoides*). These stands share boundaries, but were differentiated by US Forest Service district staff based on past management history, resulting in experimental blocking. The two western stands are located 18 km to the west and are 2 km apart from each other. These stands are more productive, with greater overall plant cover and higher site indices, and more mesic-type vegetation (understory dominated by *Carex geyeri* and forbs such as *Arnica cordifolia*). Cheatgrass was much less common in the western as compared to the eastern stands, but was documented on all stands in 2002, the earliest year we have understory vegetation data. As typical of most dry forested public lands in western North America, the stands are open to cattle grazing for approximately 6 weeks in the summer. Soils are generally dominated by Mollisols, but Inceptisols and Alfisols are also present (Carlson 1974; Hatten et al. 2008) and soil texture among the stands is quite similar (Hatten et al. 2012). Mean annual precipitation is 464 mm per year (1981–2012) with only 24% falling during the growing season (May–September; Online Reference 1).

Experimental design

This study was established in 1997 and has been described in previous work (Thies et al. 2005; Kerns et al. 2006). Prior to burning in 1997, each of the five stands was divided into three units (averaging 8 ha in size) and randomly assigned season of burn (spring, fall and unburned). In 2002 the study was expanded and the burned experimental units were bisected with one half randomly selected to be reburned every 5 years (RB) and the other half receiving only the original single burn (1B). Thus the experiment contains five treatments: control (no burning), spring RB, spring 1B, fall RB, and fall 1B. There are three 0.2 ha sample plots within each treatment (six plots in the control) that were established systematically along transect bearings in 1997. The single burn treatments as of 2012 have been burned only once in the fall of 1997 and spring of 1998. The 5-year interval fall reburns were conducted in October 1997/2002/2007, and the spring 5-year interval reburns in June 1998/2003/2008 for a total of three burns. Prescribed burns were by hand-carried drip torches using a multiple-strip head-fire pattern maintaining a 60 cm flame length if possible.

Field sampling

An array of variables were used in this analysis, which included field sampling of understory and overstory vegetation, ground cover, quantification of fire severity, and soil measurements. Detailed descriptions of methods can be found in Kerns et al. (2011) and Thies et al. (2005). Fire severity data (i.e., burn percentage, litter and duff depth, bare soil cover) were recorded after each fire (1998, 2003, 2008). The vegetation data used here were from 2002, 2004, 2007, 2009 and 2012. Vegetation measurements were designed to assess plant community responses without destructive sampling. Within each 0.2 ha plot, all trees were tallied and measured, and after each burn fire severity measurements were also collected. Current year plant canopy cover for all species was visually estimated and recorded by species to the nearest percentage point on eight 1-m^2 quadrats using a marked (0.10 m) PVC square. Quadrats were arranged 5 m and 6 m from the

plot center in each cardinal direction. Ground cover (e.g., bare soil, rock, litter, woody debris >10 cm diameter) data were also recorded.

Analysis

We tackled our first question on the effects of disturbance regime characteristics on cheatgrass cover using univariate statistics and plot-scale data from the designed experiment, which is a randomized block, incomplete split-plot with repeat measures with season of burn as the whole plot (control, fall and spring), interval of burn as the split plot (three burns every 5 years, RB; and a single burn, 1B) and year as the repeat measure. Controls are the incomplete split, as controls were not burned; however, there are six plots within the controls matching the subsampling as if they were split. Treatment was defined as the combination of burn season and frequency (e.g., fall RB). The univariate response variable cheatgrass cover was averaged at the experimental unit scale for each sampling year based on the three plots within each treatment type in each block, and analyzed with a mixed model ANOVA using Proc MIXED in SAS 9.3 and the Satterthwaite degree of freedom method and a spatial power covariance structure. Treatment and year were fixed effects and stand (block) was random. Differences were assessed with pairwise comparisons within year with alpha set at 0.05. Cheatgrass cover was log transformed after examination of residuals for normality and equality of variance. Least square (LS) means are presented as uncorrected backtransformed LS means.

Our second question asked whether local and fine-scale cheatgrass establishment and spread, and broader scale extent/impact are facilitated or constrained by disturbance, other abiotic factors, biotic resistance and propagule pressure. We used three data sets at two spatial scales and regression trees (CART, Tibco Spotfire S+ 8.2) to address this question. For the establishment and spread models we used cheatgrass cover from quadrats (1 × 1 m) within each plot (Online Resource 2). Predictor variables related to disturbance regime, other abiotic factors not directly related to burning, biotic resistance and propagule pressure are listed in Online Resource 3. The dependent variable in all three models was cheatgrass cover in 2012, but for the establishment model, a total of 67 quadrats (of 712) were identified that did not have cheatgrass in 2002 but were eventually invaded by 2012. Only 47 of these were used in the analysis because we randomly selected two non-adjacent quadrats from each plot to control for issues related to spatial autocorrelation and the fact that some predictor variables would be repeated for these quadrats because they are only available at the plot scale (e.g., fire severity, soil texture, slope and heat load). This could erroneously raise the importance of these variables in relation to the response variable in the model. For the spread model, a total of 46 quadrats were identified that had cheatgrass cover in 2002, and we randomly selected 29 of these using the same protocols as above. We note that both the local establishment and spread datasets effectively look at spread (because cheatgrass is already in the area; we are not measuring new ecosystem establishment) but differ in their initial fine-scale conditions, which may have important implications related to fine-scale invasion processes. To examine patterns related to cheatgrass extent/impact, we used mean cheatgrass cover based on all eight quadrats in 2012 from the eighty-nine 0.2 ha plots using the same predictor variables, except all variables were at the plot rather than the quadrat scale.

Results

Disturbance regime characteristics and cheatgrass cover

In 2002 prior to burning, there were no differences in cheatgrass cover in 2002 between the two interval treatments for either season (spring RB and 1B and fall RB and 1B, $P > 0.5$; Fig. 1). However, it was evident in 2002 that the initial fall burns resulted in significantly higher cheatgrass cover than most of the other treatments (all contrasts $P < 0.05$ except the fall RB and control contrast $P = 0.08$; Fig. 1). In 2004, cheatgrass cover was significantly higher following fall reburning than spring ($F_{1,21.5} = 5.13$, $P = 0.0340$) and control ($F_{1,16.3} = 7.96$, $P = 0.0121$). Even though the single burn fall treatment was not reburned, cheatgrass cover increased in 2004 and remained significantly higher than the control ($F_{1,16.3} = 7.22$, $P = 0.0160$) and spring RB treatments ($F_{1,21.5} = 4.59$, $P = 0.0437$) (Fig. 1). Again there were no differences between repeat

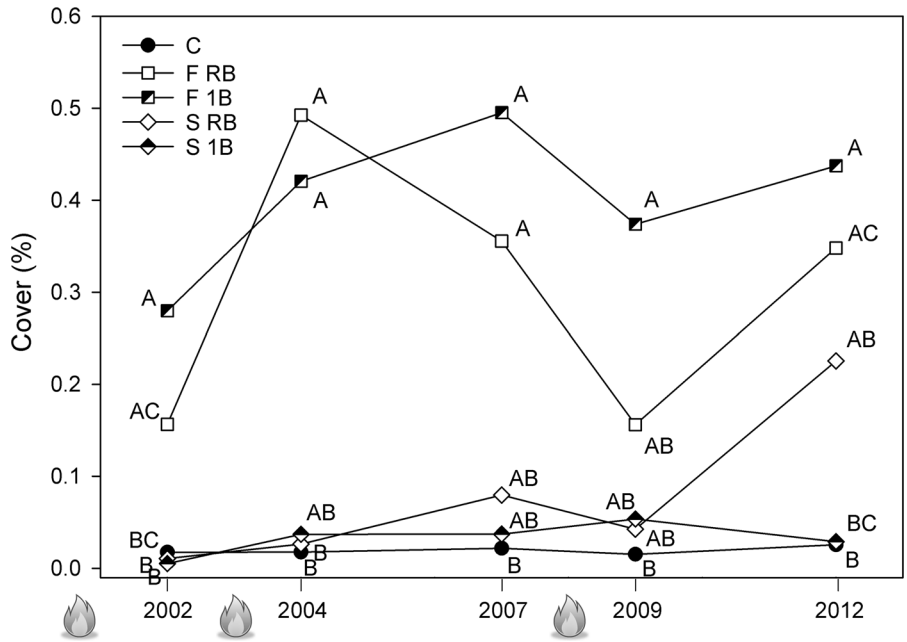

Fig. 1 Log backtransformed mean exotic annual grass (cheatgrass) cover from 2002 to 2012. The initial fires were conducted in the fall (F) of 1997 and spring (S) of 1998 (1B) and then every 5 years in the reburn (RB) treatments for a total of three burns. Controls (C) are unburned units. *Flame graphic* indicates year of burning for applicable treatments. *Uppercase letters* denote statistical significance ($P < 0.05$) among treatments within each sample year

burning and a single burn in either the fall or spring in 2004. The control and both spring treatments were statistically similar as well.

In 2007, cheatgrass cover continued to rise for the fall 1B treatment, but declined in the fall RB although both treatments were still significantly different than the control ($F_{1,16.3} = 7.01$, $P = 0.0174$; $F_{1,16.3} = 5.60$, $P = 0.0307$ respectively) (Fig. 1). Cover increased in the spring RB slightly and it was statistically similar to both the fall RB and 1B treatments. In 2009, two growing seasons after the second reburns, cover dropped in both fall treatments but remained almost the same in the other treatments. The only difference detected was that the fall 1B treatment had significantly higher cheatgrass cover than the control ($F_{1,16.3} = 7.38$, $P = 0.0150$). In 2012, fifteen years after the first burn, cheatgrass cover in the single burn fall treatment remained higher than the other treatments, significantly greater than the control ($F_{1,16.3} = 5.79$, $P = 0.0283$) and spring 1B treatments ($F_{1,21.5} = 4.41$, $P = 0.0477$), but still similar to the fall RB. Cover also rose in the fall RB, and was greater than in the control ($F_{1,16.3} = 4.90$, $P = 0.0415$). Cover rose in the spring RB treatment as well, but was not significantly different from the control ($F_{1,16.3} = 3.40$, $P = 0.083$).

Interestingly, only the spring RB and 1B treatments showed a significant increase in cheatgrass cover from 2002 to 2012 ($F_{1,26} = 15.05$, $P = 0.0006$; $F_{1,26} = 4.97$, $P = 0.0347$ respectively) although differences were <0.25% and may not be biologically significant (Fig. 1). Note that for all cover values shown in Fig. 1, back transformed means from the statistical model are presented, leading to lower cover values than those generated from the raw data.

The relative role of propagule pressure, biotic and abiotic factors

The local cheatgrass establishment model used one variable directly related to disturbance regime and a single abiotic factor to explain 68% (proportional reduction in deviance, PRD) of the variance (Fig. 2a). Cheatgrass cover in 2012 averaged 47% in quadrats where more than 85% of the plot was burned in the first burns, and where bare soil cover was <20% in 2002. But cover only averaged 15% in quadrats that had more than >20% bare soil cover in 2002. Cover averaged 8% in quadrats that did not burn as extensively (<85%) in the first fires. The cheatgrass spread model used a single variable related to biotic resistance—native annual forb cover in 2002—and explained 65% (PRD) of the variance (Fig. 2b). Higher cheatgrass cover in 2012 was associated with lower native annual forb cover in 2002. Note that on average, cheatgrass cover increased on these quadrats

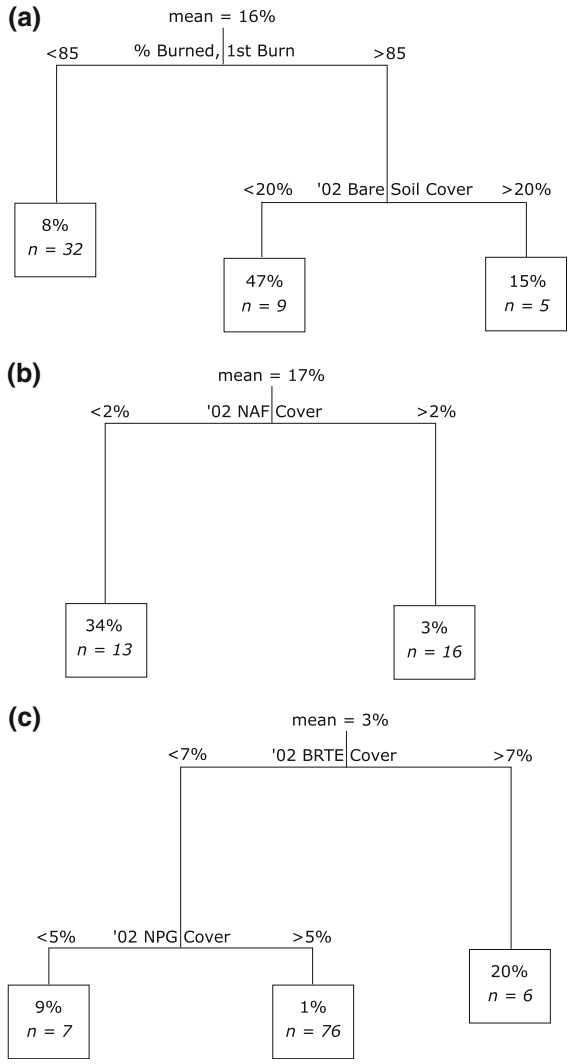

Fig. 2 Classification and regression trees explaining cheatgrass invasion (percent cover) in 2012 based on three models: **a** local establishment ($n = 47$). Only quadrats that had no cheatgrass cover in 2002 but were invaded in 2012 were included with variance explained by disturbance regime and an abiotic factor; **b** local spread ($n = 29$). Only quadrats that had cover in 2002 were included with variance explained by a single biotic resistance factor; **c** extent/impact ($n = 89$). All quadrats in 2012 were included and averaged to the plot scale, with variance explained by variables related to propagule pressure and biotic resistance. BRTE = *Bromus tectorum* (cheatgrass); NAF = native annual forb; NPG = native perennial grass

through time (mean cover in 2002 was 14%, and 17% in 2012). The cheatgrass extent/impact model used two variables related to propagule pressure and biotic resistance to explain 51% (PRD) of the variance (Fig. 2c). Cheatgrass cover in 2012 averaged 20% in areas that had >7% cover in 2002. But cheatgrass cover averaged only 1% if cover in 2002 was <7% and where 2002 native perennial grass cover was >5%. If 2002 native perennial grass cover was <5%, cheatgrass cover averaged about 9% in 2012. Note that on average, cheatgrass cover increased on the plots, rising from 1% in 2002 to 3% in 2012.

Discussion

Cheatgrass cover varied based on disturbance regime characteristics

For our first question we asked, what is the effect of disturbance regime characteristics on cheatgrass cover through time? The cover of cheatgrass varied through time based on both burn season and interval. Fall burning, regardless of frequency, tended to increase cheatgrass cover compared to the other treatments. Higher severity burn conditions are typical in the fall, and can alter resource conditions and allow invasive species to respond positively (Davis et al. 2000). Indeed, the single fall burn in 1997 appears to have "set the stage" for the patterns observed from 2002 to 2012. This result is consistent with other findings that cheatgrass increased in cover with time since fire (Shinneman and Baker 2009). However, the greatest resource fluctuations would be associated with fall reburning, yet fall reburning did not lead to increased cheatgrass cover compared to a single fall burn. While some resource fluctuations may lead to advantageous conditions for cheatgrass (e.g., short-term nutrient pulse, increased light, bare soil), other resource fluctuations may be less advantageous, such as nutrient depletion associated with repeat burning (Ojima et al. 1994; Wright and Hart 1997), which could lead to population decline. Beckstead and Augspurger (2004) demonstrated that high nitrogen availability was the main factor in sustaining cheatgrass dominance in a shadscale-bunchgrass community in the Great Basin. Cheatgrass normally has higher nutrient uptake rates (Link et al. 1995; Monaco et al. 2003) and growth rates (Arredondo et al. 1998) compared to native grasses. Interestingly, spring reburning increased cheatgrass cover from 2002 to 2012, although several reburns were required before this pattern was significant. Because spring burning was generally low severity, and burn severity decreased through time due to reduced fuels (unpublished data), frequent spring

burning may actually create conditions favorable for cheatgrass expansion. However, we caution that the differences we detected were very small. Spring burning occurred very late in this forested ecosystem (usually early June) as adequate time was needed to allow fuels to dry after snowmelt. Cheatgrass germinates in the fall and rapidly grows in the spring during snowmelt. The fires occurred when seed heads had already emerged and were mature. Seeds of many species are most vulnerable to heat damage before they are fully cured (Furbush 1953; McKell et al. 1962; DiTomaso et al. 2001). However, the cool-season native perennials were just starting their active growth and may be negatively impacted by spring burning, providing a competitive edge for cheatgrass. However, previous work has not demonstrated these negative effects in relation to spring burning (unpublished data).

Elucidating patterns in cheatgrass cover through time in relation to our treatments was confounded by wide variation in year-to-year climatic patterns. Patterns of cheatgrass abundance have been found to vary with climatic conditions, particularly low fall precipitation as cheatgrass germinates in the fall (Ashton et al. 2016). The third burns in 2007/2008 coincided with a period of historically very low average growing season precipitation (Online Resource 1), which might explain why cheatgrass increased in 2004 in response to burning, but decreased in 2009. Throughout most the 2002–2012 study period, growing season precipitation was relatively high compared to the drought years of 2007 and 2008. Cover also decreased in the fall single burn treatment in 2009, which was obviously not reburned. This supports the idea that the decrease in cheatgrass after the 2007 fall burn treatments may have largely been due to climatic factors. These trends were less obvious in the other treatments because cheatgrass cover was lower in those areas.

Factors important for cheatgrass establishment, spread and extent/impact varied

While fire, particularly fall burning, led to increased cheatgrass cover, disturbance regime variables only emerged positively in relation to cheatgrass cover in our fine-scale establishment model. Specifically, percentage area burned in the first fires emerged as the number one variable, underscoring the importance of disturbance in driving establishment under these experimental conditions. Interestingly, the highest cheatgrass cover for the establishment model was predicted where burn extent was greater than 85% but where bare soil cover five years later was less than 20%. Low bare soil (and lack of relationships with biotic resistance factors) suggests increased litter in these areas might be important. Litter is known to promote the establishment of cheatgrass and other annual bromes because of seed entrapment and moisture retention (Bansal et al. 2014; Ashton et al. 2016). However, another process may be important. Some of the quadrats with low bare soil cover (<20%) were repeatedly burned from 2002 to 2012. Areas with low bare soil cover, particularly areas subject to litter build up, can burn more intensely, which may actually provide cheatgrass with an advantage due to increased resources and/or reduced competition due to plant mortality (Bates and Davies 2014).

The spread model showed that cheatgrass can increase in areas that have low biotic resistance in the form of low native annual forb cover. Native annual forbs might be the best "analog" species for cheatgrass in this ecosystem, particularly in relation to active growth period, as there are no native annual grasses. Growth of invasive species can be suppressed by species that are similar and of the same functional type (Fargione et al. 2003; van Ruijven et al. 2003; Theoharides and Dukes 2007). These results support other recent evidence that early successional forbs can be successful in preventing exotic invasions (Abella et al. 2012; Herron et al. 2013). The survival and density of large perennial grasses is often linked to annual grass invasion resistance (Chambers et al. 2007; Davies 2008), but there is limited evidence that these native grasses completely repel invasions, particularly after disturbances such as fire, as native perennial grass recovery can take years. However, native perennial grass cover emerged as an important secondary predictor in our extent/impact model, but only when initial cheagtrass cover was low (low propagule pressure). Bansal and Sheley (2016) demonstrated that native perennial grass cover was also negatively correlated to cheatgrass extent in the Great Basin (at broad scales, $\sim$6000-km^2). Annual forbs were not correlated, but their study differed from ours in that they looked at a contemporaneous relationship. Our data indicate that perennial grasses may be important for limiting invasion extent and

impact but native annual forbs may be important for limiting initial spread at fine scales in repeatedly disturbed environments. However, the successful establishment of native annuals is often limited to specific establishment requirements linked to annual precipitation conditions, which might limit their ability to repel invasions if conditions are not optimal. After completing a meta-analysis examining the biotic resistance literature, Levine et al. (2004) concluded that biotic resistance does not repel establishment and is more important later in the invasion process, slowing the rise to dominance by the invasive species and mitigating the overall impact of invasions. Our results are very consistent with these conclusions.

While propagule pressure is often considered to strongly influence invasive species establishment and spread, the variables we used in our models that are related to propagule pressure only emerged as an important predictor variable in our broader scale extent/impact model. McGlone et al. (2011) found that factors governing invasion of native communities are complex and high propagule pressure may not always result in establishment even in areas exposed to disturbance. However, the disturbance in their study involved clipping, and there are a number of studies demonstrating no increase in annual grass invasion with actual grazing (Stohlgren et al. 1999b; Kerns et al. 2011; Ashton et al. 2016). Very little propagule pressure may be necessary for establishment to occur in "benign" (low stress, non-harsh) environments where high disturbance levels facilitate greater resource availability (Theoharides and Dukes 2007). Likewise, when abiotic resistance is high (little disturbance) establishment and spread may be less overwhelmed by high rates of propagule pressure (D'Antonio et al. 2001). But variables related to propagule pressure were important in explaining the broader scale extent of cheatgrass in our study. Similarly, Colautti et al. (2006) suggest that propagule pressure may be important for the continued success or persistence of an invader. Eschtruth and Battles (2011) point out that there is growing evidence that variability in propagule pressure is an important contributor to observed differences in the extent of invasion among communities.

In our study of cheatgrass invasion in the context of seasonal and repeat burning, we found that fall burning in particular increased cheatgrass cover, regardless of burn frequency. We found no evidence that cheatgrass invasion is decreasing through time even in areas burned only once, although cover remains at a relatively low level at the experimental scale (multiple stands), and reduction and resurgence cycles likely related to climatic factors were noted. Our regression trees describe more complex interactions among disturbance regime, other abiotic variables, biotic resistance and propagule pressure that varied based on invasion stage. The pronounced differences in predictor variables in the three modeled data sets may be explained by theories concerning the different roles that these factors play in the invasion process between disturbance regimes and other small- and large-scale abiotic and biotic processes. Disturbance and other abiotic factors facilitated cheatgrass establishment, regardless of biotic resistance and propagule pressure. While biotic resistance may not repel initial localized establishment, it may help constrain spread, extent, and subsequent impact. Native annual forbs were important for localized spread, but native perennial grass cover was linked to limiting cheatgrass extent. However, the most important factor related to cheatgrass extent in these forests in 2012 was variability in cheatgrass cover in 2002, a factor linked to propagule pressure. Our findings regarding factors affecting invasion dynamics may be useful to consider for future restoration and conservation efforts in burned ponderosa pine forests.

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