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Impacts of restoration treatments on alien plant invasion in *Pinus ponderosa* forests, Montana, USA

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Summary

1. Invasion by alien plant species represents a challenge to land managers throughout the world as they attempt to restore frequent fire-adapted ecosystems following decades of fire exclusion. In ponderosa pine *Pinus ponderosa* forests of western North America, the response of alien species to restoration treatments has not been well documented, particularly for alien species capable of altering environmental conditions (transformers). Understanding alien species dynamics is critical for developing treatments that accomplish restoration goals while minimizing alien invasion.

2. We used a replicated, randomized block experiment to compare the effects of an untreated control and thin-only, burn-only and thin-burn treatments on alien and transformer understorey species at multiple spatial scales (1 m^2, 100 m^2 and 1000 m^2). Data were collected pre-treatment and for multiple post-treatment years. We compared richness and cover of alien species and transformer species among treatments, and identified environmental variables correlated with transformer species cover. Indicator species analysis was used to identify transformer species associated with specific treatments.

3. Alien and transformer species richness and cover were significantly higher in the thin-burn than in all other treatments at all spatial scales. Thin-only and burn-only treatments showed greater alien and transformer species responses than the control at the larger 100-m^2 and 1000-m^2 scales.

4. Increased transformer cover was strongly correlated with increased tree crown scorch height and removal of overstorey trees.

5. The thin-burn treatment had four transformer species as indicators, the thin-only had one, while the burn-only and control had none.

6. *Synthesis and applications*. The results show that alien species, including transformers, respond to restoration treatments, especially the combined thin-burn treatment. Therefore monitoring for alien species invasion is an essential component of a restoration programme. Abundance of transformer species increased with increasing disturbance intensity, suggesting that less intense single-disturbance treatments (burn-only, thin-only) or incremental treatments may be preferred in some applications. Where more intense treatments are required to meet management objectives, specific strategies, such as seeding of native species, limiting grazing before and after treatment and harvesting over a protective winter snowpack, may be necessary to limit alien invasion.

Key-words: exotic species, forest management, fuel reduction, invasive plants, noxious weeds, prescribed burning, thinning

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Introduction

Fire is a historically common disturbance process in many forested ecosystems (Rodriguez-Trejo & Fulé 2003) and prescribed burning is increasingly being used to reintroduce this process to ecosystems throughout the world. For example, prescribed burning is used to address declining conditions in eucalypt (*Eucalyptus* spp.) forests in Australia (Ellis, Mount & Mattay 1980), Scots pine *Pinus sylvestris* L. forests in northern Europe (Linder, Jonsson & Niklasson 1998) and longleaf pine *Pinus palustris* P. Mill. forests in the south-eastern USA (Brockway *et al*. 2005). Restoration treatments that employ thinning, burning or both are also being recommended to improve structure and function in historically fire-adapted ponderosa pine *Pinus ponderosa* P. & C. Lawson forests of western North America that have been fire excluded for decades (Moore, Covington & Fulé 1999; Fiedler *et al*. 2001; Allen *et al*. 2002).

The associated ecosystem effects of restoration treatments have been little studied over much of ponderosa pine's 11 million-ha range (which extends from Mexico northwards to southern British Columbia, Canada), particularly regarding effects on alien understorey species. However, alien plant invasions are increasingly being recognized as a threat to the success of restoration treatments (Sieg, Phillips & Moser 2003; Wolfson *et al*. 2005). A few recent studies have documented positive responses by alien species to treatments in pine forests of Arizona (Griffis *et al*. 2001; Fulé, Laughlin & Covington 2005) and South Dakota, USA (Wienk, Sieg & McPherson 2004). To our knowledge, the experiment presented here is the first designed to focus exclusively on alien species' responses to forest restoration treatments, and the first to differentiate treatment effects on alien and transformer species.

Alien invasion depends on the number of propagules of potential invaders, characteristics of the invading species, and susceptibility of the site to invasion (Lonsdale 1999). Treatments may enhance community invasibility by introducing propagules of exotic species (Harrod 2001) and imposing disturbance, which creates safe sites and reduces competition (Hobbs & Huenneke 1992; Petryna *et al*. 2002). Thinning (Kaye & Hart 1998) and burning (DeLuca & Zouhar 2000) treatments can also increase resource availability, which may facilitate invasion (Huenneke *et al*. 1990; Davis, Grime & Thompson 2000; Leishman & Thomson 2005) and provide alien species with a competitive advantage (Kolb *et al*. 2002; Brooks 2003). The combination of resource addition and decreased competition may have the greatest potential to facilitate invasion (Thompson *et al*. 2001; Minchinton & Bertness 2003), especially if propagule pressure also increases.

Invasion by alien plant species is only one post-disturbance recolonization scenario (Hobbs & Huenneke 1992). Indeed, there are instances where thinning and burning in pine forests have not led to alien invasion (Fulé *et al*. 2002; Fornwalt *et al*. 2003) and in some cases fire reduces alien abundance (Smith & Knapp 1999; Emery & Gross 2005). The outcome depends on community and environmental attributes, herbivory, stochastic factors and characteristics of the disturbance itself (Halpern 1988; Alpert, Bone & Holzapfel 2000), therefore different restoration treatments may have differential effects.

Alien species invasions pose threats to ecosystems throughout the world (Vitousek *et al*. 1996; Mack *et al*. 2000; Brooks *et al*. 2004); however, all alien species do not have equivalent impacts (Ortega & Pearson 2005; Williamson & Fitter 1996). A subset of alien species, which Richardson *et al*. (2000) terms 'transformers', has the potential to alter ecosystem properties. Because of their capacity to counteract restoration efforts, limiting the response of these species is pivotal to restoration success. However, sampling design influences alien and transformer detection, as invasion patterns can vary with spatial scale (Halpern & Spies 1995; Stohlgren, Bull & Otsuki 1998) and time since disturbance (Meiners, Pickett & Cadenasso 2002; Wienk, Sieg & McPherson 2004; Fulé, Laughlin & Covington 2005).

Our study evaluated four treatments in second-growth ponderosa pine forests: untreated (control), prescribed burning in the spring (burn-only), thinning (thin-only) and thinning followed by prescribed spring burning (thin-burn). It presented a unique opportunity to assess the effects of restoration treatments on alien invasions in a randomized and replicated field experiment. To thoroughly document alien response, we sampled over multiple years and spatial scales. We further evaluated a subset of alien species (transformers) because of their potentially profound ecosystem impacts. Our study addressed three key questions. (i) Do restoration treatments differ in their degree of invasion by alien and transformer species as measured by cover and richness? (ii) What environmental variables are correlated with increased transformer cover? (iii) Are individual transformer species associated with specific treatments?

Methods

The study was established on the 11 000-ha University of Montana Lubrecht Experimental Forest, which was located at 47°N, 113°W in western Montana, USA. The altitude of the study sites ranged from 1263 m to 1388 m a.s.l. Mean annual air temperature was 7 °C and mean annual precipitation was 50 cm, nearly half of which fell as snow (Nimlos 1986). We established three blocks of 36 ha each in second-growth stands comprised primarily of ponderosa pine and Douglas-fir *Pseudotsuga menziesii* (Mirbel) Franco, with lesser amounts of western larch *Larix occidentalis* Nutt. and lodgepole pine *Pinus contorta* Dougl. ex Loud. Most trees were 80–90 years old, with scattered clumps of regeneration and occasional trees up to 200 years old. Cattle grazing had been a traditional land use throughout the past century. Despite only modest grazing pressure

 Journal of Applied Ecology, **43**, 887–897

in recent decades, study sites were fenced to isolate treatment effects on alien species invasion.

The three blocks were located about 3 km apart. Each block was subdivided into four square 9-ha treatment units. One replicate of each treatment was then randomly assigned within each block, with the exception of two burn treatment units that were strategically located to allow containment of prescribed burns. Ten 20×50-m (1000 m^2) modified Whittaker plots were established within each treatment unit, using a stratified random design to ensure dispersion. Each Whittaker plot was subdivided into 10 10×10-m (100 m^2) subplots. Each subplot had two 1×1-m (1 m^2) quadrats located in opposite corners (20 quadrats $plot^{-1}$), 12 of which were randomly selected to sample understorey vegetation.

TREATMENTS

Restoration treatments were developed to move forest density and structure towards historical conditions (Metlen & Fiedler 2006). The treatment referred to as thin-only consisted of silvicultural felling designed to reduce the density of small- and medium-sized trees, and leave an open fire-resistant stand composed primarily of seral species. Unfelled trees were marked to achieve a target reserve basal area (BA) of 11 m^2 ha^{-1}, which resulted in about half of the basal area being removed. Large-diameter ponderosa pine were favoured as unfelled trees, although some pine trees were retained in all size classes, if available. Logging slash (non-merchantable tree tops and limbs) was left on site and driven over by the harvesting equipment to condense fuel accumulations. Thinning was conducted during the winter of 2001 on a snowpack.

Prescribed broadcast burns were implemented during May and June of 2002, with a separate prescribed burn for each of the six burn treatment units (3 × burn-only and 3 × thin-burn). Burning was conducted using a strip-head fire technique (Kilgore & Curtis 1987). Relative humidity during burning ranged from 20% to 48%, temperatures from 9 °C to 29 °C, and winds from 2 km h^{-1} to 13 km h^{-1}. Flame lengths varied from 0·2 to 1·2 m in the burn-only and from 0·2 to 2·7 m in the thin-burn.

VEGETATION SAMPLING

All species present on each plot (1000 m^2) and associated quadrats (1 m^2) were identified prior to treatment in the summers of 2000 (thin-only and thin-burn) and 2001 (burn-only and control) and after treatment in 2002, 2003 and 2004. Over the course of the study, 178 native species and 25 alien species were recorded. Nomenclature followed the USDA PLANTS database (USDA-NRCS 2004), which was also used to determine if plants were alien or native. Alien species are listed in Appendix S1 in the supplementary material.

Cover was visually estimated for each species at the quadrat level (1 m^2). Pre-treatment cover was estimated using cover codes (0, 0%; 1, < 1%; 2, 1–10%; 3, 11–25%; 4, 26–50%; 5, 51–75%; and 6, 76–100%). For analysis, cover codes were converted to the median value for the code. Post-treatment cover was estimated to the nearest percentage, which is more sensitive than codes for temporal trend analysis, especially for rare species (Stohlgren, Bull & Otsuki 1998).

Noxious weed lists and the literature were used to identify a subset of alien species (transformers; *sensu* Richardson *et al*. 2000) that can alter environmental conditions and therefore are a priority for management. These species included *Bromus tectorum* L., *Carduus nutans* L., *Centaurea biebersteinii* DC., *Cirsium arvense* (L.) Scop., *Cirsium vulgare* (Savi) Ten., *Cynoglossum officinale* L., *Potentilla recta* L. and *Verbascum thapsus* L. In addition to the data collected at the 1000-m^2 and 1-m^2 scales, cover of transformer alien species was also visually estimated on each of the 10 subplots (100 m^2) per plot in 2003 and 2005 to provide further insights into transformer species invasion. A cover value of 0·2 was assigned to each species in a subplot with < 0·5% cover; species cover was estimated to the nearest percentage thereafter. The cover of exposed mineral soil at the subplot level was estimated in the same way.

BA was calculated pre-treatment and in 2003 for each overstorey tree > 10 cm diameter at breast height (d.b.h. = 1·37 m), and summed for each plot (1000 m^2). Saplings (trees > 1·37 m in height but < 10 cm in d.b.h.) were censused on five randomly selected 100-m^2 subplots per plot prior to treatment and in 2003. The proportional change in overstorey BA (m^2 ha^{-1}) and sapling density (stems ha^{-1}) was calculated by subtracting the post-treatment value from the pre-treatment value and dividing the difference by the pre-treatment value. In 2003, live canopy cover was sampled by densitometer at the 18 subplot corners in each plot.

Post-treatment cover was estimated to the nearest percentage at the quadrat level (1 m^2) for duff (i.e. partially decomposed and fully humified organic matter) and litter, rock, woody stems (live and dead stems > 1 m in height), natural wood (downed woody debris large enough to obstruct growth) and logging slash. In 2002, maximum crown scorch height was measured for every tree > 10 cm d.b.h. in a plot. Slope and aspect were measured for each plot, and effective aspect was calculated following Stage (1976).

STATISTICAL ANALYSIS

Prior to analysis, a significance level of $P = 0{\cdot}05$ was set for all tests. Treatment differences in alien and transformer species richness and cover were tested using blocked multi-response permutation procedures (BMRPP) in PC-ORD version 4 (McCune & Mefford 1999). Data were summarized at the treatment unit level ($n = 3$) prior to statistical analysis. Richness and cover were tested for treatment differences using a median alignment for block and a Euclidean distance measure, with each year (pre-treatment, 2002, 2003 and 2004) tested separately. Blocking with median alignment focuses the analysis on differences among treatments but does not provide a test statistic for a block effect (Mielke & Iyer 1982). Alien richness was tested at two spatial scales, 1000 m^2 and 1 m^2, while cover data were tested at the 1-m^2 scale only. Transformer species were evaluated similarly. The additional data on transformer species cover collected at the 100-m^2 scale in 2003 and 2005 were tested for treatment differences within each year.

Similar in purpose to ANOVA, MRPP is a technique that tests for differences among groups based on the measure of distance (or dissimilarity) between pairs of observations (Zimmerman, Goetz & Mielke 1985). However, assumptions of normality and equal variance among groups are not required with MRPP (Zimmerman, Goetz & Mielke 1985). An estimate of effect size is given by the chance-corrected within-group agreement (A), which ranges from zero to one. If all observations within a treatment are identical, A will equal one; however, if the observed mean equals the expected, A is zero.

Using MRPP, pair-wise comparisons with three replicates would not result in a meaningful *P*-value. Therefore, when the overall test for treatment differences was significant, data associated with each treatment were averaged at the plot level ($n = 30$) for between-treatment comparisons. Comparisons were performed using univariate MRPP tests without blocking. We are confident in the results because neither the thinning nor burning treatments were homogeneous across units, plot centres were separated by a minimum of 70·7 m, and tests for overall treatment effect had already shown significance. Pair-wise comparisons were Bonferroni-adjusted (significance level $P/6 = 0{\cdot}0083$).

Environmental and treatment-related variables correlated with transformer species cover were identified using univariate multiple regression in SPSS version 12·0 (SPSS Inc., Chicago, IL). Transformer species' cover data at the subplot level (100 m^2) were averaged to the plot level for all analyses ($n = 30$). All environmental variables were also averaged to the plot level prior to analysis. The plot level was used to account for variation within treatment units, because extremes may be more influential than averages (Underwood 1997). Cover of transformer species in 2003 and 2005 was used as a response variable, with a separate regression performed for each year. A rich model was fitted and stepwise backwards elimination was conducted until only significant ($P < 0{\cdot}05$) explanatory variables remained. Explanatory variables are listed in Appendix S2 in the supplementary material. A treatment variable was deliberately not included in these analyses to isolate environmental attributes that may facilitate transformer invasion. Levene's test for homogeneity of variance, scatterplots and normal probability-probability plots (P-P plots) were used to assess assumptions.

An indicator species analysis (Dufrêne & Legendre 1997) was conducted in PC-ORD version 4 (McCune & Mefford 1999) to compare how individual transformer species performed among treatments. This technique produces an indicator value (IV) for every species based on cover and frequency, where the IV ranges from 0 to 100, with 100 being a perfect indicator. Subplot-level (100 m^2) transformer cover data from 2003 and 2005 were averaged up to the plot level ($n = 30$), which provided a more accurate estimate of frequency for each species than averaging to the treatment unit level ($n = 3$). Separate analyses were performed for data collected in 2003 and 2005.

Results

TREATMENT EFFECTS

There were no among-treatment differences in richness or cover of either alien species or transformer species prior to treatment, but numerous differences after, indicating differential responses to alternative restoration treatments. Between-year comparisons within treatments were not performed because of pre- and post-treatment differences in cover estimation.

ALIEN RICHNESS AND COVER

Alien richness differed among treatments at the 1000 m^2 scale in all post-treatment years (Table 1). Pair-wise comparisons revealed that in 2002 the thin-only and thin-burn treatments both had significantly higher alien richness than the burn-only and control. In 2003, alien richness in the thin-only treatment remained higher than the control, while the thin-burn had higher alien richness than all other treatments. This same trend continued in 2004.

At the 1-m^2 scale, alien richness did not differ among treatments in 2002 (Table 1). In 2003 and 2004, there were marginally significant differences among treatments ($P = 0{\cdot}053$ and $P = 0{\cdot}052$, respectively). The thin-burn had significantly higher alien richness at the 1-m^2 scale than all of the other treatments in these years, based on pair-wise comparisons. Alien cover was significantly different among treatments in 2003 and marginally different among treatments in 2004 ($P = 0{\cdot}052$; Table 1). In both years, the thin-burn had higher alien cover than all other treatments.

TRANSFORMER SPECIES RICHNESS AND COVER

Following treatment, transformer species richness at the 1000-m^2 scale differed among treatments in each sampling year (Table 2). The thin-only and thin-burn had significantly higher richness in 2002 than the burn-only and control. In 2003, transformer richness in the thin-only remained higher than the burn-only and control, while the thin-burn had higher transformer

Table 1. Mean alien species richness and cover (SE; $n = 3$), by treatment, for each sample year. BMRPP was used to test for treatment differences for each variable in each year ($n = 3$). Where significant differences existed, MRPP tests of plot-level data were used for pair-wise comparisons ($n = 30$). Treatments that were significantly different within a year are denoted with different letters (Bonferroni corrected $P < 0.0083$)

	Control	Burn-only	Thin-only	Thin-burn	A†	*P*
1000-m² richness						
Pre-treatment	2·17(0·66)	1·60(0·75)	2·33(0·68)	2·60(1·14)	0·01	0·440
2002	3·03(0·96)a	2·37(0·87)a	4·80(1·14)b	5·13(1·36)b	0·47	0·017*
2003	3·73(0·84)a	4·83(1·17)ab	6·23(1·19)b	9·37(1·89)c	0·55	0·005**
2004	4·40(0·89)a	5·93(2·03)ab	6·93(1·07)b	10·20(2·67)c	0·22	0·034*
1-m² richness						
Pre-treatment	0·17(0·07)	0·19(0·12)	0·23(0·08)	0·27(0·15)	–0·15	0·801
2002	0·18(0·08)	0·18(0·14)	0·26(0·10)	0·41(0·16)	0·10	0·207
2003	0·21(0·09)a	0·28(0·17)a	0·33(0·11)a	0·71(0·27)b	0·25	0·053‡
2004	0·30(0·13)a	0·47(0·21)a	0·41(0·15)a	1·28(0·55)b	0·24	0·052‡
Percentage cover						
Pre-treatment	0·14(0·07)	0·14(0·10)	0·58(0·30)	0·22(0·15)	0·27	0·068
2002	0·19(0·08)	0·20(0·17)	0·37(0·15)	0·55(0·25)	0·11	0·188
2003	0·24(0·09)a	0·34(0·23)a	0·44(0·16)a	1·95(1·10)b	0·22	0·024*
2004	0·33(0·14)a	0·59(0·27)a	0·58(0·25)a	2·44(1·29)b	0·18	0·052‡

$*P < 0.05$, $**P < 0.01$.
†A in MRPP is the chance corrected within-group agreement (see text).
‡P < 0·055 was considered marginally significant; therefore post-hoc tests were performed.

Table 2. Mean transformer species richness and cover (SE; $n = 3$), by treatment, for each sample year. MRPP was used to test for treatment differences for each variable in each year ($n = 3$). Where significant differences existed, MRPP tests of plot-level data were used for pair-wise comparisons ($n = 30$). Treatments that were significantly different within a year are denoted with different letters (Bonferroni corrected $P < 0.0083$)

	Control	Burn-only	Thin-only	Thin-burn	A†	*P*
1000-m² richness						
Pre-treatment	0·50(0·15)	0·60(0·38)	0·57(0·27)	0·83(0·43)	–0·03	0·543
2002	0·70(0·10)a	0·73(0·44)a	1·63(0·33)b	2·20(0·66)b	0·38	0·023*
2003	0·80(0·06)a	1·40(0·42)a	2·50(0·32)b	3·60(0·55)c	0·67	0·004**
2004	1·10(0·17)a	2·07(0·75)b	2·87(0·32)b	4·20(0·67)c	0·48	0·012*
1-m² richness						
Pre-treatment	0·03(0·01)	0·07(0·06)	0·08(0·05)	0·05(0·04)	–0·02	0·595
2002	0·04(0·02)a	0·07(0·07)ab	0·08(0·06)ab	0·13(0·06)b	0·29	0·027*
2003	0·03(0·02)a	0·09(0·08)ab	0·10(0·07)ab	0·23(0·09)b	0·46	0·014*
2004	0·05(0·03)a	0·14(0·07)a	0·12(0·07)a	0·60(0·27)b	0·36	0·029*
Percentage cover						
Pre-treatment	0·04(0·02)	0·08(0·07)	0·38(0·30)	0·07(0·06)	0·07	0·123
2002	0·05(0·02)a	0·09(0·09)ab	0·15(0·09)ab	0·20(0·12)b	0·21	0·045*
2003	0·06(0·03)a	0·16(0·15)a	0·18(0·11)a	1·21(0·74)b	0·26	0·016*
2004	0·08(0·04)a	0·25(0·14)a	0·21(0·11)a	1·43(0·79)b	0·27	0·031*

$*P < 0.05$, $**P < 0.01$.
†A in MRPP is the chance corrected within-group agreement (see text).

species richness than all other treatments. By 2004, both the burn-only and thin-only had higher transformer richness than the control, while the thin-burn maintained higher transformer richness than all other treatments.

Treatments also differed in transformer species richness at the 1-m² scale in each post-treatment sampling year (Table 2). In 2002 and 2003, the thin-burn had significantly higher richness than the control. In 2004, the thin-burn had significantly higher transformer richness than all other treatments. Transformer species cover at the 1-m² scale was also significantly higher in the thin-burn than the control in 2002, and was significantly higher in the thin-burn than all other treatments in 2003 and 2004 (Table 2).

Transformer cover at the subplot level differed among treatments in 2003 ($P = 0.025$) and 2005 ($P = 0.032$; Fig. 1). In both years, the thin-only and burn-only had significantly higher transformer species cover than the control. The thin-burn had significantly higher transformer cover than all other treatments in 2003, and higher cover than the thin-only and control in 2005.

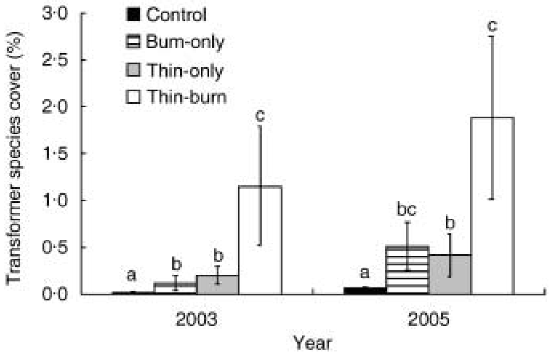

Fig. 1. Treatment means and standard errors (n = 3) for transformer species cover at the subplot level (100 m^2) in each treatment in 2003 and 2005. BMRPP was used to test for treatment differences within years (n = 3). Where differences occurred, pair-wise MRPP tests of plot-level data (n = 30) were used to test for between-treatment differences (represented by different letters). Pair-wise comparisons were adjusted by a Bonferroni procedure.

TRANSFORMER COVER AND ENVIRONMENTAL VARIABLES

Four environmental variables explained 43% of the variation in transformer species cover in 2003, and five variables accounted for 47% of the variation in 2005 (Table 3). In both years, transformer cover varied significantly among the three blocks, and was positively correlated with overstorey tree basal area removal and increasing crown scorch height. Parameter estimates revealed that, in both years, a 60% reduction in overstorey basal area would elicit nearly a 1% increase in transformer cover. With each 10 m of crown scorch height in 2003 and 7 m of scorch height in 2005, transformer cover would be expected to increase by 1%. In 2003, the relationship of transformer cover to saplings was opposite to that of overstorey trees, although sapling density was a much less significant explanatory variable. In 2005, transformer species cover was positively correlated with the cover of duff and litter, and of slash.

INDICATOR SPECIES

The indicator species analysis revealed the thin-burn had four significant transformer indicators (*Carduus nutans*, *Cirsium arvense*, *Cirsium vulgare* and *Verbascum thapsus*) in both 2003 and 2005 (Table 4). The only other significant indicator, *Cynoglossum officinale*, was an indicator of the thin-only in both 2003 and 2005. There were no transformer species indicators for either the control or burn-only treatments.

Discussion

The active restoration treatments in our study (thinning, burning or both) increased the abundance of alien and transformer species. A response was evident even though these species were very minor constituents of the understorey community initially. Our results are consistent with those from studies in ponderosa pine forests of other regions where invasion was facilitated by management treatments (Griffis *et al*. 2001; Wienk, Sieg & McPherson 2004; Fulé, Laughlin & Covington 2005). Similar relationships have been documented following harvest in coastal Pacific north-west forests, USA (Thysell & Carey 2001) and southern Canadian boreal forests (Haeussler *et al*. 2002), and following prescribed burning in Australia (Milberg & Lamont 1995) and South America (Petryna *et al*. 2002). The operational scale at which we implemented treatments, coupled with a replicated and randomized experimental design, which is rare in studies of forest stand manipulations (Bennett & Adams 2004), instil confidence in the differential responses of alien and transformer species in our study. However, follow-up analyses with n = 30 (including pair-wise comparisons) are limited in inference to our study site, and should be extrapolated with caution.

A clear pattern emerged in all the analyses, with invasion greatest in the combined thin-burn treatment,

Table 3. Final regression models for transformer species cover and environmental and treatment-related explanatory variables in 2003 and 2005. A parsimonious model was identified through stepwise backward elimination

Parameter	β	t	P
2003			
Intercept	0·10	0·67	0·506
Block†			0·001**
Proportional change in basal area	1·63	4·45	0·000**
Crown scorch height	0·10	5·43	0·000**
Proportional change in sapling density	–0·56	–2·03	0·045*
R^2 = 0·429			
2005			
Intercept	–4·22	–2·60	0·010*
Block†			0·016*
Proportional change in basal area	1·48	2·89	0·005**
Crown scorch height	0·14	5·64	0·000**
Percentage cover of duff and litter	0·06	2·65	0·009**
Percentage cover slash (tops and limbs)	0·11	3·28	0·001**
R^2 = 0·472			

*P < 0·05, **P < 0·01.
†Block was treated as a categorical variable, and an extra sums-of-squares F-test was used to ascertain significance.

Table 4. Indicator species analyses of supplemental subplot-level (100 m^2) cover of transformer species, collected in 2003 and 2005 only. Indicator values (IV) range from 0 to 100, with 100 being a perfect indicator of a treatment. *P*-values represent the probability of obtaining an IV as large or larger by chance, based on a Monte Carlo test with 1000 randomizations

	2003			2005		
Species	Treatment	IV	*P*	Treatment	IV	*P*
Bromus tectorum	Thin-burn	5·0	0·644	Control	7·6	0·566
Carduus nutans	Thin-burn	52·4	0·001**	Thin-burn	56·5	0·001**
Centaurea biebersteinii	Thin-only	25·3	0·243	Thin-only	31·1	0·238
Cirsium arvense	Thin-burn	26·5	0·005**	Thin-burn	31·5	0·002**
Cirsium vulgare	Thin-burn	71·3	0·001**	Thin-burn	62·4	0·001**
Cynoglossum officinale	Thin-only	24·4	0·003**	Thin-only	23·3	0·017*
Potentilla recta	Thin-burn	17·3	0·323	Thin-burn	19·1	0·406
Verbascum thapsus	Thin-burn	63·4	0·001**	Thin-burn	71·9	0·001**

*$P < 0·05$, **$P < 0·01$.

least in the control, and intermediate in the single active treatments (burn-only and thin-only). The much greater response of alien, and especially transformer, species to the thin-burn treatment was supported by multiple sources of evidence. For example, by 2004 alien cover in the thin-burn was more than four times the cover in any other treatment and more than seven times the cover in the control. Differences in cover of transformer species in 2004 were even more striking, as the thin-burn had more than five times the transformer cover of any other treatment, and more than 17 times the cover of the control. In addition, the thin-burn had numerous transformer species as indicators compared with the other treatments. Similarly, Wienk, Sieg & McPherson (2004) found that certain alien species had significantly higher biomass in treatments that involved partial harvesting and burning than in those that had neither treatment or only one treatment. Griffis *et al*. (2001) also reported significantly higher alien forb richness in treatments that were thinned and burned than in those that were untreated or thinned only.

The response in the thin-burn may have been the result of increased frequency of disturbance (Hobbs & Huenneke 1992; Ross *et al*. 2004), with two separate disturbance events in two consecutive years. However, the regressions of transformer cover on environmental variables suggest that the intensity of treatment also played a role. Overstorey tree reduction and increasing scorch height were strongly correlated with increased transformer cover in both 2003 and 2005. Many trees in the thin-burn were removed in the thinning and some additional trees died following burning, resulting in the largest reduction of overstorey trees of any treatment (data not shown). Also, the cut-to-length harvest system used to implement the thinning treatment left logging slash on site, which increased surface fuels and burn intensities in localized areas relative to the burn-only treatment. For example, the average crown scorch height in the thin-burn was more than 50% higher than in the burn-only (10·9 m vs. 7·0 m). Intense burning in slash piles can also create localized conditions that favour alien species (Haskins & Gehring 2004; Korb, Johnson & Covington 2004) and increase the germination and growth of certain aliens (Wolfson *et al*. 2005). Therefore, the increased intensity of the combined thin-burn treatment probably contributed to increased transformer species cover, a pattern consistent with other reports (Crawford *et al*. 2001; Griffis *et al*. 2001; Haeussler *et al*. 2002).

Increased alien invasion in the thin-burn may also be the result of increased availability of limiting resources (Davis, Grime & Thompson 2000). Thinning and burning treatments increase resource availability (Kaye & Hart 1998; DeLuca & Zouhar 2000), and removing overstorey competition in ponderosa pine forests can increase availability of limiting resources for the understorey (Riegel, Miller & Krueger 1992). For example, Gundale *et al*. (2005) studied soil nitrogen status at our site and found significantly higher total inorganic nitrogen (TIN) in the thin-burn than in any other treatment, and further found that certain alien species were correlated with high TIN (Gundale *et al*. 2006), providing evidence for the resource limitation model of alien invasion.

Noxious weed lists can be used to identify a subset of alien species that are likely to impact native communities (Skinner, Smith & Rice 2000; Ortega & Pearson 2005). Five of the eight species considered transformers in this study were recently classified as strong invaders in the inland north-west, USA (Ortega & Pearson 2005), and all eight were identified as possible noxious weed invaders following restoration treatments in south-western USA pine forests (Sieg, Phillips & Moser 2003). Strong invaders, such as the transformer species in this study, may drive changes in the community that have negative impacts on native species (Ortega & Pearson 2005). These species can trigger environmental changes that favour continued growth of the aliens themselves, including changes in fire regimes (Brooks *et al*. 2004) and below-ground processes (Ehrenfeld, Kourtev & Huang 2001). Alien species may also collectively set back natural regeneration of the dominant tree species (Keeley 2006). For example, *Cirsium vulgare* has been

 Journal of Applied Ecology, **43**, 887–897

found to reduce growth of ponderosa pine seedlings (Randall & Rejmánek 1993). However, the identity of the dominant invaders may also change over time and with changing environmental conditions (Thompson *et al.* 2001; Ortega & Pearson 2005), requiring continued vigilance in identifying species likely to complicate restoration efforts. Other species in the northern Rocky Mountains that are not designated as noxious may also have the ability to invade both disturbed and undisturbed sites (Weaver, Gustafson & Lichthardt 2001). These potential role changes illustrate the need for monitoring and updating transformer species' classifications.

The ability to detect invasion differed with spatial scale (Tables 1 and 2 and Fig. 1). For example, richness and cover in the burn-only and thin-only differed from the control at the 100-m^2 and 1000-m^2 scales but not at the 1-m^2 scale. While only the thin-burn differed from the other treatments at the 1-m^2 scale, continuing invasion from 2003 to 2004 was evident in this treatment at the 1-m^2 scale but not the 1000-m^2 scale. Alien species richness in the thin-burn nearly doubled from 2·7 times the pre-treatment level in 2003 to 4·8 times that level in 2004 at the 1-m^2 scale, while barely changing from 2003 to 2004 at the 1000-m^2 scale. Our results support the recommendation by Stohlgren, Bull & Otsuki (1998) that a more complete understanding of invasion dynamics requires sampling at multiple spatial scales.

Our analyses showed that alien and transformer species were increasing from year to year in the control as well as the treated areas, although at a lesser rate. The only exception was cover in the thin-only, which probably decreased because of physical obstructions from slash, although interannual climatic variability and a change from using cover codes pre-treatment to percentage cover post-treatment may also have contributed. Increased richness and cover in the other treatments may have been because of an underlying rate of invasion across the landscape that was further expedited by active treatments. The proximate location of control units to active treatment units (in which significant invasion was documented) may have subsequently increased propagule pressure on the control as well. Because this was a large interdisciplinary study, the heavy human traffic on these sites from researchers may also have increased propagule pressure.

Regression analysis indicated that transformer species cover was different among blocks, even after other environmental variables were accounted for in the models. Despite these differences, the relative ranking of transformer cover among treatments was similar in all blocks. Blocks in this study were within 3 km of each other, had similar fire, grazing and *c*. 1900 logging histories, and were on gentle to moderate slopes at similar altitudes. Therefore, alien invasion may have been influenced by differences among treatment applications (such as intensity) and stochastic processes, as well as subtle environmental differences not measured in this study, suggesting caution in the extrapolation of the results to other locations where conditions differ.

Further study is needed across the full range of ponderosa pine and other fire-adapted ecosystems (e.g. longleaf pine and eucalypt) where thinning and prescribed burning treatments are employed to understand the implications of restoration treatments over a range of environments and stand histories. Variations in treatment, such as harvest system and season of burning (Emery & Gross 2005), also have differential effects that warrant further investigation.

While decreasing alien abundance with time has been documented in other studies (Meiners, Pickett & Cadenasso 2002; Petryna *et al*. 2002), this trend was not yet evident at our study site, where transformer abundance increased in all treatments from 2003 to 2005. Similarly, Fulé, Laughlin & Covington (2005) found significantly higher alien cover in restoration treatments than in untreated areas 5 years after treatment application in south-western USA ponderosa pine forests. The ability of aliens to persist at least several years following treatment and to contribute heavily to the seed bank (Halpern, Evans & Nielson 1999) may complicate future restoration efforts, especially given that restoration treatments are not a one-time event but a series of re-entries (disturbances) over time (Arno *et al*. 1995; Allen *et al*. 2002). Conversely, the initial disturbances resulting from restoration treatments are probably the most intense, given that treatments must address many decades of vegetation development since the last disturbance (Arno *et al*. 1995). Further study and monitoring are needed to better understand the longer-term consequences of alien invasion.

Synthesis and applications

Alien and transformer species increased in all restoration treatments, underscoring the importance of post-treatment monitoring for early detection of invasion so that problematic treatments can be modified (Harrod 2001). The significant response of alien species in the thin-burn treatment presents a management dilemma because of the multiple benefits that accrue with this treatment, which include killing fire-vulnerable Douglas-fir seedlings and saplings, reducing unnaturally high fuel build-ups, recycling nutrients bound in slash and down woody material and increasing the sprouting of important wildlife forage species. Land managers must weigh the benefits of restoration treatments against unwanted side-effects relative to their specific situations and management objectives. Although the response of alien species in this study was significant, it was modest in real terms (about a 2% increase in cover in the thin-burn) and similar to the 2–3% increase reported by Fulé, Laughlin & Covington (2005) 5 years after implementing a full thin-and-burn restoration treatment in Arizona, USA. Three years post-treatment, aliens comprised 8% of the total plant cover in the thin-burn, the most intense treatment in our study. In contrast, Crawford *et al*. (2001) reported that alien species comprised 26% of the total plant cover following wildfire in an Arizona ponderosa pine forest. Paradoxically, doing nothing or applying treatments that are not effective in reducing fire hazard may lead to even more invasion after stand-replacing wildfire (Griffis *et al*. 2001).

Transformer abundance was positively correlated with variables that indicate greater treatment intensity. If higher intensity treatments are necessary to accomplish restoration goals, then specific management strategies to reduce alien invasion may be required. For example, Korb, Johnson & Covington (2004) found that soil amendments and seeding with native plant species reduced alien plant dominance after intense burning of slash piles in south-western USA pine forests. Conducting thinning treatments over a winter snowpack can also reduce or eliminate soil disturbance (Gundale *et al*. 2005) and is a viable option over most of ponderosa pine's range. Limiting grazing by domestic animals several years before and after treatments is an additional strategy to limit invasion (Keeley 2006). On sites where intense treatments are not required, application of single treatments (burn-only or thin-only) or incremental treatments designed to move gradually toward more historical conditions (Allen *et al*. 2002) may be used to limit alien invasion.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from http://w.w.w.blackwell-synergy.com.

Appendix S1. Alien species.

Appendix S2. Environmental variables.