Establishment of non-native plant species after wildfires: effects of fuel treatments, abiotic and biotic factors, and post-fire grass seeding treatments

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Abstract. Establishment and spread of non-native species following wildfires can pose threats to long-term native plant recovery. Factors such as disturbance severity, resource availability, and propagule pressure may influence where non-native species establish in burned areas. In addition, pre- and post-fire management activities may influence the likelihood of non-native species establishment. In the present study we examine the establishment of non-native species after wildfires in relation to native species richness, fire severity, dominant native plant cover, resource availability, and pre- and post-fire management actions (fuel treatments and post-fire rehabilitation treatments). We used an information-theoretic approach to compare alternative hypotheses. We analysed post-fire effects at multiple scales at three wildfires in Colorado and New Mexico. For large and small spatial scales at all fires, fire severity was the most consistent predictor of non-native species cover. Non-native species cover was also correlated with high native species richness, low native dominant species cover, and high seeded grass cover. There was a positive, but non-significant, association of non-native species with fuel-treated areas at one wildfire. While there may be some potential for fuels treatments to promote non-native species establishment, wildfire and post-fire seeding treatments seem to have a larger impact on non-native species.

Additional keywords: Colorado; New Mexico; ponderosa pine; prescribed fire; rehabilitation; thinning.

Introduction

Frequent, low intensity fire has historically been a significant disturbance in semi-arid forests of the western United States (Swetnam and Baisan 1996; Brown *et al*. 1999). Fire regimes and forest structure have been dramatically altered as a result of management practices in the 19 and 20th centuries, notably in south-western ponderosa pine (*Pinus ponderosa* P. & C. Lawson) ecosystems (Covington and Moore 1994; Fule *et al*. 1997). Currently, fuel loads in many of these forests are uncharacteristically high, and wildfire is suppressed, resulting in a fire regime of infrequent, large, and severe wildfires (Covington and Moore 1994; Fule *et al*. 1997). These large and severe wildfires are associated with a variety of undesirable ecological effects, including increased tree mortality (McHugh and Kolb 2003), reduced understory plant cover (Armour *et al*. 1984; Griffis *et al*. 2001), and increased mortality in the soil seed bank (Korb *et al*. 2004; Wienk *et al*. 2004). The resulting high incidence of exposed bare soil and low tree canopy cover creates a high potential for establishment of non-native species, increased water runoff, and soil erosion in post-fire environments.

Fuel reduction treatments, such as thinning of trees and prescribed burning, are commonly used to reduce the potential for severe wildfires (Covington *et al*. 1997; Kalabokidis and Omi 1998; Stone *et al*. 1999). While these treatments are often successful in reducing fire severity (Pollet and Omi 2002), they may have other adverse ecological effects. Particularly, movement of equipment and personnel into remote areas may facilitate spread of non-native plant propagules, and establishment of populations. Non-native species may also be more likely to thrive in treated or burned areas where availability of resources, such as light and nitrogen, is typically higher (DeBano *et al*. 1998; Kaye and Hart 1998).

Land managers also commonly implement various treatments after severe wildfires, to mitigate the risks of increased runoff and soil erosion, and establishment of non-native species. One of the more commonly used post-fire treatments is application of large amounts of grass seed in the hope of

rapidly establishing vegetative cover (Robichaud *et al.* 2000). These treatments have been controversial because non-native species are often used in these efforts, and the overall effectiveness of such treatments has been questioned (Robichaud *et al.* 2000; Beyers 2004). The intentional introduction of non-native species may have adverse effects on native plant recovery. In addition, these treatments may lead to the unintentional introduction of other non-native species as seed mixes are often contaminated with non-native species not intended to be in the seed mixes.

Appropriate post-treatment and post-fire management may curb establishment of non-native species. In particular, rapid detection of non-native species may allow for eradication of individuals before populations establish. Rapid detection of non-native species would be facilitated by knowledge of factors that best predict where non-native species establish after wildfires. In other studies, consistent factors have been shown to be good predictors of non-native species' presence or cover at different scales. Factors that have proven to be important predictors for non-native species, on a landscape scale, include soil fertility (Stohlgren *et al.* 1999*a*, 1999*b*), disturbance severity (Stylinski and Allen 1999; Crawford *et al.* 2001; Griffis *et al.* 2001), dominant native species cover (Smith and Knapp 1999; Huston 2004; Smith *et al.* 2004), non-native species propagule pressure (Lonsdale 1999; Levine 2001; Brown and Peet 2003), and native species richness (Stohlgren *et al.* 1999*a*; Bruno *et al.* 2004). These same factors should be important in post-fire environments. For example, disturbance may be enhanced through fire severity and fuel treatments, and propagule pressure of non-native species may be higher near roads, and with the use of post-fire seeding treatments through contamination of mixes with non-native species. On a much smaller scale ($1\,m^2$) biotic factors such as plant cover and propagule pressure and small-scale disturbance can impact establishment of non-native species (Kotanen 1997; Levine 2001; Smith *et al.* 2004). These factors may also be important in post-fire environments as fire severity impacts understory plant cover, and post-fire seeding impacts propagule pressure of non-native species.

Dominant native species that produce high vegetative cover often have the greatest potential to deter establishment of non-native species at small scales (Huston 2004; Smith *et al.* 2004). In our study systems, perennial grasses make up a majority of the understory biomass and thus have the greatest potential for deterring non-native species establishment. However, grass cover is often significantly reduced following high severity wildfires. While non-native seeded grasses are introduced to combat low vegetation cover (and consequent soil erosion) after fire, their effects may be very different than native grasses. Often, seeding treatments do not result in high vegetative cover, and grass seed mixes are often contaminated with other non-native species (Robichaud *et al.* 2000; Beyers 2004). Thus, such treatments can essentially act to increase the propagule pressure of non-native species,

without supplying the high grass productivity that may prevent establishment of non-native species. Evaluation of the interactions between native and seeded grasses, and other non-native species, is necessary to understand what post-fire management actions may best deter establishment of non-native species. These interactions may be most important at small scales where effects of direct plant–plant interactions are significant.

The objective of the present study was to examine the effects of pre-fire fuel treatments, post-fire rehabilitation treatments (seeding), high severity wildfire, and other abiotic and biotic factors on establishment of non-native plant species after severe wildfires. We addressed several competing hypotheses to determine which factors are most important in determining successful establishment of non-native species after wildfires. Specifically, we addressed the following hypotheses:

1. H_{A1}: Fuel treatments (thinning and prescribed fire) increase the likelihood for non-native species establishment.
2. H_{A2}: Abiotic factors associated with wildfire (fire severity, canopy cover, and nitrogen) increase the likelihood for non-native species establishment.
3. H_{A3}: Biotic factors (vegetative cover, propagule pressure, and species richness) control the likelihood for non-native species establishment.
4. H_{A4}: Other abiotic factors (percent slope, incident radiation, clay content, distance to streams and roads) control the likelihood for non-native species establishment.
5. H_{A5}: A combination of these factors control the likelihood of non-native species establishment.

We tested these competing hypotheses by collecting data on vegetation at different spatial scales at three wildfires in Colorado and New Mexico, USA in areas that experienced varying pre-fire fuel treatments and post-fire management activities.

Methods

Study sites

We sampled three wildfires in the course of the present study: the 2000 Cerro Grande fire, the 2000 Hi Meadow fire, and the 2002 Hayman fire. Each fire occurred in low-elevation forests of the eastern Rocky Mountains, burned at least 4000 ha with variable severity, and included both pre- and post-fire management activities within the fire perimeter. All burned areas had similar disturbance history in terms of logging and livestock grazing (Allen 1989; Veblen and Lorenz 1991).

Cerro Grande

The Cerro Grande fire was management ignited on 4 May 2000 in Bandelier National Monument near Los Alamos, New Mexico. The fire went out of prescription on 5 May and

high winds on subsequent days prevented control until 8 June. The fire reached a final size of 193 km^2. The fire burned into areas where the Santa Fe National Forest had done extensive fuel-reduction treatments since 1994. The treatments included mechanical thinning and prescribed burning, both in isolation and in combination. Grass seed was aerially applied to areas that were classified as high and moderate fire severity (80 km^2) in an attempt to increase vegetation cover and thus, reduce the potential for increased runoff and erosion (see Appendix 1). Elevation ranged from 2000 to 3140 m. Ponderosa pine (*Pinus ponderosa* P. & C. Lawson) is dominant with pinyon pine (*Pinus edulis* Englem.) and oneseed juniper (*Juniperus monosperma* (Englem.) Sarg.) abundant at lower elevations, and white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex. Hildebr.) and Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) abundant at higher elevations. We sampled this area in the summer of 2001.

Hi Meadow

The Hi Meadow fire started on 12 June 2000 from an undetermined ignition source on private land in Park County, Colorado, in the Southern Rocky Mountains. Before containment on 20 June, the fire grew to a size of 44 km^2. Approximately half the burn area was on the Pike National Forest, which had accomplished fuel treatments since 1990, involving both prescribed fire and mechanical thinning on ~12.5 km^2. After the fire, grass seed was applied by hand or with a seed drill on ~12.5 km^2 (see Appendix 1). Elevation ranged from 2150 to 2500 m. Ponderosa pine is dominant in the canopy, with lodgepole pine (*Pinus contorta* Dougl. ex. Loud.), and Douglas-fir also present. We sampled this area in the summer of 2002.

Hayman

The Hayman fire ignited on 8 June 2002, from an illegal campfire on the Pike National Forest in Park County, Colorado. The fire remained active until 28 June, by which time it had burned 554 km^2. Management activities had occurred on ~81 km^2 within the burn area, though we focused on the prescribed fire and mechanical thinning activities conducted since 1990. Post-fire aerial seeding occurred on ~130 km^2 (see Appendix 1). Elevation ranged from 2150 to 2500 m. Ponderosa pine and Douglas-fir are dominant in the canopy, with lodgepole pine also present. We sampled this area in the summer of 2003.

Data collection

Sample points within each study area were selected randomly within several strata. Landscape stratification was accomplished with Arcview GIS software (ESRI 1999) and existing spatial data layers. Strata included vegetation type (including pre-fire fuel treatment status), aspect, burn severity (including unburned reference areas within 300 m of the

fire perimeter), and post-fire mitigation activities (with a focus on seeding). Areas that had been subject to management activity prior to 1990 were avoided, as were areas that were subject to post-fire activities other than seeding (e.g. herbicides or felling). At least three plots were sampled within each stratum.

We established a modified-Whittaker plot at each sampling point (Stohlgren *et al.* 1998). The modified-Whittaker plot is multi-scale and has one 100 m^2 plot, two 10 m^2 plots and ten 1 m^2 quadrats nested within 1000 m^2. Our sampling objectives focused on assessments of fire severity, soil and topographic variables, and cover and height measurements for vascular plant species. To estimate fire severity at a scale relevant to understory plants, a rating of depth of ground char (adapted from Ryan and Naste 1985) was assigned to each of the ten 1 m^2 quadrats within the modified-Whittaker plot. This rating is based on char and consumption of litter, duff and woody debris, the color of the soil surface, and the depth of ground char. Canopy cover, which is likely to be a function of fire severity, was measured using a densiometer. We took four readings in different cardinal directions in the center of each plot. Soil samples (5–15 cm depth) were collected from the corners and center of each modified-Whittaker plot, pooled, and analysed for indicators of nutrient (total carbon and nitrogen) and water (texture) availability. Topographic variables considered at all sites were map distances from the nearest road and the nearest stream (m), slope steepness (%), direct incident radiation (MJ/cm^2/year) (McCune and Keon 2002), and elevation (m).

Botanists identified and measured the cover and height of all species in each 1 m^2 subplot. Cover was also recorded for any non-plant surface items encountered (i.e. wood, water, rock, roots, duff/litter, lichen, moss, soil, trail/road, dung, and other [trash, bones, etc.]). Botanists then searched the 10 m^2, 100 m^2, and 1000 m^2 plots for any species not previously recorded, and noted them as present for richness assessments. Plants that could not be identified to species were collected off-plot and pressed for later identification. Species were classified as non-native according to the Natural Resources Conservation Service Plants Database (USDA NRCS 2006). Plants that could not be identified because of growth stage retained their unknown name for use in richness analyses. Vegetation data were grouped according to biotic predictor variables most likely to impact non-native species cover, i.e. cover of dominant native species (native grass cover), propagule pressure of non-native species through application of potentially contaminated seed mixes (seeded grass cover), and native species richness. Species included in these groups are listed in Appendix 1.

Data analysis

We employed standard statistical software (SAS Institute 2001) and an information-theoretic approach (Burnham and

Anderson 2002) for the development and selection of multiple linear regression, ANOVA, and ANCOVA models to explain landscape and small-scale variations in non-native species cover. Several models were constructed and compared using an information theoretic framework (Burnham and Anderson 2002). Rather than testing an individual alternative hypothesis against a null hypothesis, this framework allows one to evaluate the evidence for multiple, competing alternative hypotheses by comparing statistical models that represent these different hypotheses. We compared several models that represented our hypotheses of interest. The specific hypotheses we addressed were that non-native species cover was mainly a function of biotic variables (native grass cover, seeded grass cover, and native species richness), abiotic variables resultant from wildfire (mean char depth, canopy cover, mulch cover, and total nitrogen), treatment variables (thinned, prescribe burned, thinned + prescribed burned, and no fuel treatment), other abiotic variables (distance from streams, distance from roads, slope, incident radiation, and percentage of clay content), and a combination of these variables. Models at the $1000\,m^2$ scale included variables from each of the competing hypotheses, and then combinations of these variables. At the $1\,m^2$ scale, we constructed models that included biotic variables that were more likely to be important at this scale (native grass cover, seeded grass cover, and species richness) and abiotic variables that were measured at this scale (char depth and bare soil exposure).

Akaike's Information Criterion (AICc) was calculated for each constructed model, and the model with the lowest AICc was assumed to be the best predictor of non-native species cover. When several models showed strong support in the data (AICc within 7 points of the model with the lowest AICc value), these models were averaged with Akaike weights to obtain averaged parameter estimates and associated standard error values (Burnham and Anderson 2002). The mean and standard error values from parameters in the best (or averaged best) models were then used to calculate 95% confidence intervals, where 95% CI = mean ± (1.96*SE). Unlike other model selection methods (i.e. stepwise, backward), AICc imposes a penalty for each increase in the number of model parameters. This facilitates selection of simple models with strong support in the data, and reduces the chances of selecting models with statistically significant but ecologically spurious parameters (Burnham and Anderson 2002). If several models have strong support based on the data, parameter estimates from all the models can be averaged using Akaike weights (Burnham and Anderson 2002).

Results

Cerro Grande

Pre-fire fuel treatments occurred only in the ponderosa pine forests within the burned area, while our sampling plots spanned a broader elevational gradient of the burned landscape, and included mixed conifer and pinyon-juniper forests. Because this design did not allow us to stratify samples to test the effects of an interaction between vegetation type and fuel treatment on non-native species, we conducted separate analyses for plots in ponderosa pine forests (including fuel treatments) and plots in other parts of the landscape (mixed conifer, pinyon-juniper, and untreated ponderosa pine forests). Elevation was included as a variable to account for the different vegetation types. At the $1000\,m^2$ scale in ponderosa pine forests, the best models accounted for up to 42% of the variability in non-native species cover and included a fuel treatment effect, seeded grass cover, native grass cover, native species richness, percent slope, incident radiation, and percent clay content (Table 1). All selected models were significant at the level of $P < 0.001$. All parameter estimates, except for native species richness, had 95% confidence intervals that overlapped zero. Non-native species cover was positively associated with native species richness. Non-native species cover also seems to be mostly negatively associated with native grass cover and percent slope. Non-native species cover also appeared higher in areas that were thinned prior to the wildfire, although confidence intervals for estimates of non-native cover overlapped for areas that were thinned, prescribed burned, thinned and prescribed burned, and received no fuel treatment prior to the wildfire.

In other portions of the burned landscape, at the $1000\,m^2$ scale, two models showed considerable support based on the data and attributed up to 31% of the variability in non-native species cover (Table 1). Parameter estimates in these models included canopy cover, char depth, total nitrogen, seeded grass cover, native grass cover, and native species richness. Non-native species cover was positively associated with seeded grass cover and native species richness. 95% confidence intervals for all other parameter estimates overlapped zero. Non-native species cover was mostly positively associated with char depth, and negatively associated with native grass cover.

In ponderosa pine forests, at the $1\,m^2$ scale, three models showed considerable support based on the data and attributed up to 6% of the variability in non-native species cover at this scale (Table 2). All selected models were significant at the level of $P < 0.01$. Parameter estimates in these models included native grass cover, seeded grass cover, native species richness, bare ground exposure, and char depth. However, only 95% confidence intervals for estimates of seeded grass cover and native species richness did not overlap zero. Non-native species cover was positively associated with both seeded grass cover and native species richness. Non-native species cover was mostly positively correlated with char depth, and negatively correlated with native grass cover and bare soil exposure.

In other portions of the burned landscape, at the $1\,m^2$ scale, three models showed considerable support based on the

Table 1. Models and parameter estimates for non-native species cover at the 1000 m² scale at the Cerro Grande wildfire

For ponderosa pine forests, $n = 38$, for other portions of the burned landscape, $n = 53$. For ponderosa pine plots, model 1 is an ANOVA model, models 5, 8, 9, and 11 are ANCOVA models, and models 2, 3, 4, 6, 7, and 10 are multiple linear regression models. For all other plots, all seven models are multiple linear regression models. Selected models (in bold) were those with strong support in the data. Parameter estimates in bold are associated with 95% confidence intervals (CI) that do not overlap zero. AICc, Akaike's Information Criterion; Int, intercept; seed, seeded grass cover (%); grass, native grass cover (%); rich, native species richness; slope, slope (%); rad, incident radiation (MJ/cm²/year); clay, soil clay content (%); can, canopy cover (%); N, total soil nitrogen (%); burn, least square mean for non-native cover in ponderosa pine areas that were treated prior to wildfire with prescribed burn; thin, least square mean for non-native cover in ponderosa pine areas that were treated prior to the wildfire with thinning; Th/bu, least square mean for non-native cover in ponderosa pine areas that were treated prior to the wildfire with thinning and prescribed fire; none, least square mean for non-native cover in ponderosa pine areas that received no fuel treatment prior to wildfire; elev, elevation (m); strm, distance from nearest stream (m); road, distance from nearest road (m)

Model	Adjusted r^2	AICc	Parameter	Estimate[A]	95% CI
Ponderosa pine plots					
Int + treat	**0.24**	**124**	Int	−0.51	−15.90, 14.93
Int + can + char + N	0.01	136	Seed	0.08	−0.22, 0.38
Int + slope + rad + clay	0.09	130	Grass[B]	−1.36	−3.48, 0.76
Int + grass + seed + rich	**0.28**	**121**	**Rich**	**0.35**	**0.16, 0.54**
Int + treat + can + char + N	0.17	133	Slope	−0.20	−0.45, 0.05
Int + char + can + N + seed + grass + rich	0.27	126	Rad	−0.35	−20.20, 19.50
Int + slope + rad + clay + seed + grass + rich	**0.42**	**118**	Clay	0.24	−0.15, 0.63
Int + treat + seed + grass + rich	**0.40**	**121**	Burn	3.81	−0.51, 8.14
Int + treat + slope + rad + clay	0.20	134	Thin	10.49	7.86, 13.11
Int + can + char + N + slope + rad + clay	0.00	139	Th/bu	6.33	2.30, 10.35
Int + all variables	0.52	129	None	6.95	3.44, 10.47
Other plots					
Int + canopy + char + N	0.12	113	Int	−0.86	−3.68, 1.97
Int + slope + rad + clay + elev + strm + road	0.05	121	Can	0.00	−0.03, 0.03
Int + grass + seed + rich	**0.31**	**101**	Char	0.76	−0.30, 1.82
Int + char + can + N + grass + seed + rich	**0.31**	**104**	N[B]	−1.72	−6.70, 3.25
Int + slope + rad + clay + elev + strm + road + grass + seed + rich	0.32	109	**Seed**	**0.22**	**0.08, 0.36**
Int + slope + rad + clay + elev + strm + road + can + char + N	0.14	119	Grass	−0.42	−1.01, 0.18
Int + all variables	0.31	115	**Rich**	**0.14**	**0.06, 0.22**

[A]Averaged parameter estimates from selected models; [B]square-root transformed prior to analysis.

Table 2. Models and parameter estimates for non-native species cover at the 1 m² scale at the Cerro Grande wildfire

For models in ponderosa pine forests, $n = 240$, for models in other plots, $n = 550$. The response variable and all the parameters were arcsine square-root transformed prior to analysis. All models are single or multiple linear regression models. Selected models (in bold) were those with strong support in the data. All selected models were significant at the $P < 0.01$ level. Parameter estimates in bold are associated with 95% CI that do not overlap zero. See Table 1 for parameter abbreviations

Model	Adjusted r^2	AICc	Parameter	Estimate[A]	95% CI
Ponderosa pine plots					
Int + seed	**0.05**	**−236**	Int	0.13	−0.23, 0.50
Int + grass	0.02	−230	**Seed**	**0.16**	**0.04, 0.28**
Int + rich	0.00	−227	**Rich**	**0.21**	**0.01, 0.41**
Int + char + soil	**0.03**	**−233**	Grass	−0.11	−0.23, 0.01
Int + seed + grass + rich	**0.05**	**−238**	Char	0.28	−0.04, 0.59
Int + all variables	**0.06**	**−237**	Soil	−0.10	−0.24, 0.04
Other plots					
Int + seed	0.01	−986	Int	0.06	−0.08, 0.20
Int + grass	**0.02**	**−994**	Seed	0.03	−0.05, 0.11
Int + rich	0.00	−984	**Rich**	**0.12**	**0.05, 0.19**
Int + char + soil	0.02	−989	**Grass**	**−0.09**	**−0.15, −0.03**
Int + seed + grass + rich	**0.04**	**−998**	Char	0.04	−0.06, 0.14
Int + all variables	**0.03**	**−995**	Soil	0.00	−0.06, 0.06

[A]Averaged parameter estimates from selected models.

Table 3. Models and parameter estimates for non-native species cover at the 1000 m^2 scale at the Hi Meadow fire

For all models, $n = 92$. Model 1 is an ANOVA model. Models 5, 8, 9, and 11 are ANCOVA models. Models 2, 3, 4, 6, 7, and 10 are multiple linear regression models. Selected models (in bold) were those with strong support in the data. All selected models were significant at the $P < 0.0001$ level. Parameter estimates in bold are associated with 95% CI that do not overlap zero. See Table 1 for parameter abbreviations

Model	Adjusted r^2	AICc	Parameter	Estimate[A]	95% CI
Int + treat	0.00	341	Int	−2.65	−11.77, 6.47
Int + char + can + N	**0.25**	**312**	**Char**	**4.31**	**2.53, 6.09**
Int + slope + clay + road + strm + rad	0.09	332	Can	−0.02	−0.08, 0.04
Int + grass + seed + rich	0.00	339	N	4.17	−4.64, 12.99
Int + treat + char + can + N	0.24	317	Seed[B]	−0.41	−1.09, 0.27
Int + char + can + N + grass + seed + rich	**0.29**	**310**	**Grass**	**0.18**	**0.00, 0.36**
Int + slope + clay + road + strm + rad + grass + seed + rich	0.07	338	Rich	0.06	−0.05, 0.17
Int + treat + grass + seed + rich	0.00	345	Slope	−0.03	−0.12, 0.06
Int + treat + slope + clay + road + stre + rad	0.08	337	Rad	1.81	−3.65, 7.27
Int + char + can + N + slope + clay + road + strm + rad	**0.30**	**311**	Clay	0.31	−0.21, 0.83
Int + all variables	0.34	317	**Road**	**0.01**	**0.00, 0.01**
			Strm	0.00	−0.01, 0.00

[A]Averaged parameter estimates from the selected models; [B]square-root transformed prior to analysis.

Table 4. Models and parameter estimates for non-native species cover at the 1 m^2 scale at the Hi Meadow fire

For all models, $n = 920$. Models predict the arcsine square-root transformation of non-native species cover. All models are single or multiple linear regression models. All predictor variables were arcsine square-root transformed prior to analysis. The selected models (in bold) had the strongest support in the data. Parameter estimates in bold are associated with 95% CI that do not overlap zero. See Table 1 for parameter abbreviations

Model	Adjusted r^2	AICc	Parameter	Estimate[A]	95% CI
Int + seed	0.01	−1029	Int	−0.05	−0.20, 0.10
Int + grass	0.01	−1033	**Seed**	**−0.14**	**−0.22, −0.06**
Int + rich	0.00	−1025	**Grass**	**−0.07**	**−0.13, −0.01**
Int + char + soil	0.05	−1066	Rich	0.10	−0.02, 0.22
Int + seed + grass + rich	0.02	−1042	**Char**	**0.31**	**0.21, 0.41**
Int + all variables	**0.07**	**−1082**	Soil	0.00	−0.06, 0.06

[A]Parameter estimates from the selected model.

data and attributed up to 4% of the variability in non-native species cover at this scale (Table 2). All selected models were significant at the level of $P < 0.01$. Parameter estimates in these models included native grass cover, seeded grass cover, native species richness, bare ground exposure (%) and char depth. However, only 95% confidence intervals for estimates of native species richness and native grass cover did not overlap zero. Non-native species cover was positively associated with native species richness, and negatively associated with native grass cover.

Hi Meadow

Eleven models were tested to predict cover of non-native species at the Hi Meadow fire at the 1000 m^2 scale. Three models showed considerable support based on the data and accounted for up to 30% of the variability in non-native species cover (Table 3). All selected models were significant at the level of $P < 0.0001$. All variables except for a treatment effect were included in the best models. Only three variables (char depth, native grass cover, and distance from

roads) had parameter estimates with 95% confidence intervals that did not overlap zero. Non-native species cover was positively associated with char depth, native grass cover, and distance from roads.

Six models were tested to predict non-native species cover at the Hi Meadow fire at the 1 m^2 scale. Only one model (the global model) showed considerable support based on the data and accounted for 7% of the variability in non-native species cover (Table 4). All selected models were significant at the level of $P < 0.0001$. Three variables, seeded grass cover, native grass cover, and char depth, had parameter estimates with 95% confidence intervals that did not overlap zero. Non-native species cover was negatively associated with seeded grass cover and native grass cover, and positively associated with char depth.

Hayman

Eleven models were tested to predict cover of non-native species at the 1000 m^2 scale at the Hayman fire. Two models showed considerable support based on the data and accounted

Table 5.   Models and parameter estimates for non-native species cover at the 1000 m² scale at the Hayman fire

For all models, $n = 102$. Model 1 is an ANOVA model. Models 5, 8, 9, and 11 are ANCOVA models. Models 2, 3, 4, 6, 7, and 10 are multiple linear regression models. Selected models (in bold) were those with strong support in the data. All selected models were significant at the $P < 0.0001$ level. Parameter estimates in bold are associated with 95% CI that do not overlap zero. Mulch, percent cover of straw mulch. See Table 1 for other parameter abbreviations

Model	Adjusted r^2	AICc	Parameter	Estimate[A]	95% CI
Int + treat	0.00	−91	**Int**	**−0.87**	**−1.46, −0.29**
Int + char + can + N + mulch	0.04	−138	Char	0.16	−0.02, 0.34
Int + slope + clay + road + rad + strm	0.04	−137	Can	0.00	−0.01, 0.00
Int + grass + seed + rich	0.26	−126	N	1.09	−0.15, 2.33
Int + treat + char + can + N + mulch	0.03	−133	Seed[B]	−0.03	−0.33, 0.26
Int + char + can + N + mulch + grass + seed + rich	**0.26**	**−161**	Grass[B]	0.03	−0.11, 0.17
Int + slope + clay + road + rad + strm + grass + seed + rich	**0.22**	**−155**	**Rich**	**0.02**	**0.01, 0.03**
Int + treat + grass + seed + rich	0.24	−120	Slope	0.00	−0.01, 0.01
Int + treat + slope + clay + rad + road + strm	0.03	−132	Rad	0.05	−0.36, 0.46
Int + char + can + N + mulch + slope + clay + rad + road + strm	0.05	−133	Clay	0.01	−0.03, 0.05
Int + all variables	0.23	−144	Road	0.00	0.00, 0.00
			Strm	0.00	0.00, 0.00
			Mulch[B]	0.03	−0.03, 0.09

[A]Averaged parameter estimates from the selected models; [B]square-root transformed prior to analysis.

Table 6.   Models and parameter estimates for non-native species cover at the 1 m² scale at the Hayman fire

For all models, $n = 1060$. Models predict the arcsine square-root transformation of non-native species cover. All models are multiple linear regression models. The selected model (in bold) had the strongest support in the data. All variables were arcsine square-root transformed prior to analysis. Parameter estimates in bold are associated with 95% CI that do not overlap zero. See Tables 1 and 5 for parameter abbreviations

Model	Adjusted r^2	AICc	Parameter	Estimate[A]	95% CI
Int + seed + mulch	0.01	−1584	Int	−0.04	−0.16, 0.23
Int + grass + rich	0.06	−1638	**Seed**	**0.14**	**0.04, 0.24**
Int + char + soil	0.01	−1584	Mulch	−0.02	−0.06, 0.18
Int + all variables	**0.06**	**−1648**	**Rich**	**0.22**	**0.16, 0.20**
			Grass	−0.01	−0.07, 0.20
			Soil	**−0.05**	**−0.09, −0.01**
			Char	**0.11**	**0.01, 0.21**

[A]Parameter estimates from the selected model.

for up to 26% of the variation in non-native species cover (Table 5). All selected models were significant at the level of $P < 0.0001$. All variables except a treatment effect were included in the best models. Only one variable, native species richness, had a parameter estimate with a 95% confidence interval that did not overlap zero. Non-native species cover was positively associated with native species richness. Non-native species cover was mostly positively correlated with char depth and total nitrogen.

Four models were tested to predict non-native species cover at the 1 m² scale at the Hayman fire. Only one model (the global model) showed considerable support based on the data and it accounted for 6% of the variability in non-native species cover (Table 6). All selected models were significant at the level of $P < 0.0001$. Four variables, seeded grass cover, native species richness, bare soil, and char depth, had parameter estimates with 95% confidence intervals that did not overlap zero. Non-native species cover was positively associated

with seeded grass cover, native species richness, and char depth, and negatively associated with bare soil exposure.

Discussion

Fuel treatments (thinning and prescribed fire) have some potential to promote establishment of non-native plant species. The literature surrounding the effects of fuel treatments on establishment of non-native species indicates a high potential based on disturbance theory (Sieg *et al.* 2003), but very little evidence for high establishment and spread rates of non-native species following fuel treatments (Griffis *et al.* 2001; Fornwalt *et al.* 2003; Abella and Covington 2004; Wienk *et al.* 2004). Our results confirm that there is a potential for higher establishment of non-native species in thinned areas, as we found a slightly higher incidence of non-native species in thinned areas in the Cerro Grande fire. However, these results were not significant. In addition, we found no significant effect of fuel treatments on non-native species

cover at either the Hi Meadow or Hayman fires, indicating that the overall potential for establishment of non-native species following fuel treatments is low in these systems.

In our study, wildfires had a greater impact on the establishment of non-native species than fuel treatments. There are many documented cases in which intense wildfires resulted in increased establishment of non-native species (Crawford *et al.* 2001; Griffis *et al.* 2001; Keeley *et al.* 2003). In our study, depth of char, an indicator of fire intensity, was a consistent predictor of higher non-native species cover at all fires and both spatial scales. Fire severity was a much more important predictor of non-native species establishment than other abiotic variables that have proven to impact non-native species establishment in other studies. Results from the present study suggest that the occurrence of large and severe wildfires may be one of the more important mechanisms for continued spread of non-native species in semi-arid forests in the west. However, fuel treatments can also result in high intensity wildfires on a smaller scale, and this may facilitate establishment of non-native species. For example, burning of slash piles, which can result in high fire intensity on a local scale, has been shown to promote establishment of non-native species (Korb *et al.* 2004).

Low explanatory power of regression models is common in small-scale plots, especially when overall vegetation cover is low and species of interest are rare (Stohlgren *et al.* 1999*a*, 1999*b*). Large-scale plots often provide better explanatory power for cover of non-native species because variability in small-scale plots is reduced (Stohlgren *et al.* 1999*a*, 1999*b*). Cover of vegetation is low immediately after wildfires, and non-native species are relatively rare, as they have had little time to invade. Thus, it is not surprising that we found low explanatory power for our plots at the $1\,m^2$ scale. However, trends found in $1\,m^2$ plots still provide valuable information on non-native species establishment on a small scale. This scale is particularly relevant for examining direct plant–plant interactions that may influence non-native species establishment (Corbin and D'Antonio 2004).

Broad application of seed mixes following fire may promote establishment of non-native species. Although the seed mixes have purity standards, there is usually some contamination with other non-native species. While the number of contaminated seeds may be small on a percentage basis, the application of very large amounts of seed (thousands of pounds) ensures that a significant number of non-native plant seeds are distributed over the landscape. Results from our study show that non-native species cover was positively associated with seeded grass cover. The Hi Meadow fire showed a deviation from this trend and we suspect that is because of the method of seed application. At the Cerro Grande and Hayman fires, seed mixes were aerially applied and resulted in very low cover of seeded grasses, a result that is often seen with broad-scale aerial application (Robichaud *et al.* 2000). At the Hi Meadow fire, seed mixes were applied by hand or

with a seed drill and resulted in very high cover of seeded grasses in a smaller portion of the burned landscape. Often, high cover of a dominant species can deter establishment of other species, both native and non-native (Smith *et al.* 2004). In this case, higher cover of the seeded grasses may have acted to deter establishment of non-native species.

High cover of dominant native species can also deter establishment of non-native species. At all fires, where cover of native grasses, the dominant understory species, was high, cover of non-native species was low. Our research suggests that post-fire treatments that encourage high vegetative cover without introducing new non-native species in contaminated seed mixes would best prevent further spread of non-native species. Hand application of native grass seed mixes or non-persistent non-native species may be preferable to broad-scale aerial application of non-native grass seed. Other erosion control treatments may be more appropriate altogether. While we examined the effects of straw mulch at only one fire (Hayman), we found no effect of mulch application on establishment of non-native species. Mulch application has also been shown to be more effective than seeding in controlling post-fire erosion (Wagenbrenner 2003).

Native species richness has been a consistent predictor of non-native species cover and richness in natural settings (Stohlgren *et al.* 1999*a*; Brown and Peet 2003). Results from our study are consistent with this trend. Some have suggested that plant dominance is the underlying driver of this relationship, with plant diversity (native and exotic) decreasing when a dominant species is present and has high productivity (Huston 2004; Smith *et al.* 2004). When no dominant species occurs, an area is more easily colonized by both native and non-native species, resulting in a positive association between native and non-native species richness. While we did not address the relationship between dominance and diversity *per se*, our results are consistent with these predictions, as we found positive relationships between non-native species cover and native species richness, and negative relationships between non-native species cover and dominant native plant cover.

While disturbance is likely to decrease understory productivity in the short term, and increase the potential for non-native species establishment, disturbance is also important for native species diversity (Petraitis *et al.* 1989). The balance between managing disturbance for diversity and non-native species can be maintained through appropriate management actions. Some factors that control non-native species invasion after disturbance are disturbance severity and propagule pressure (Stylinski and Allen 1999; Levine 2000; Crawford *et al.* 2001). In the context of fire, disturbance severity may be controlled through fuel treatments that reduce future wildfire severity. Propagule pressure of non-native species may be controlled by limiting introduction of non-native species after wildfires through erosion control measures. For those non-native species that do establish, rapid

detection may allow for better control of non-native species before populations become established.

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Appendix 1.   Species included in species groups used in data analysis

Native grasses include grasses native to the study areas. Seeded grasses include grasses used in post-fire seeding treatments.
Non-native species include all non-native species encountered in the study areas

Native grasses	Seeded grasses	Non-native species
Achnatherum hymenoides[A]	*Bromus carinatus*[A]	*Aegilops cylindrica*[A,E]
Achnatherum lettermanii[A]	*Elymus trachycaulus*[A,B]	*Agropyron cristatum*[A]
Achnatherum nelsonii[B,C]	*Festuca trachyphylla*[B,D]	*Agropyron repens*[B,E]
Achnatherum robustum[C]	*Hordeum vulgare*[A,C,D]	*Amaranthus retroflexus*[B,C]
Achnatherum scribneri[C]	*Lolium perenne*[A,D]	*Anthemis cotula*[C,E]
Agropyron albicans[B,C]	*Pascopyrun smithii*[B]	*Arabis hirsuta*[A,B,C]
Agrostis exarata[B]	*Trisetum aestivum*[C,D]	*Asperugo procumbens*[B]
Agrostis scabra[A,B,C]		*Avena sativa*[B]
Andropogon gerardii[A]		*Bromus erectus*[B]
Aristida arizonica[A]		*Bromus hordeaceus*[B,C]
Aristida longiseta[A]		*Bromus inermis*[A]
Bouteloua curtipendula[A,B,C]		*Bromus secalinus*[C]
Bouteloua gracilis[A,B,C]		*Bromus tectorum*[A,B,C,E]
Bromopsis lanatipes[B]		*Camelina microcarpa*[B,C]
Bromus ciliatus[B,C]		*Capsella bursa-pastoris*[A,E]
Calamagrostis purpurascens[B]		*Carduus nutans*[B,C,E]
Danthonia parryi[B,C]		*Cerastium vulgatum*[B]
Deschampsia caespitosa[B,C]		*Chenopodium album*[A,B,C]
Dichanthelium linearifolium[B]		*Chorispora tenella*[A,E]
Digitaria sanguinalis[C]		*Cirsium arvense*[B,C,E]
Elymus canadensis[B]		*Cirsium vulgare*[A,E]
Elymus elymoides[A,B,C]		*Conringia orientalis*[B,C]
Elymus trachycaulus[C]		*Dactylis glomerata*[B]
Festuca arizonica[B]		*Descurainia sophia*[A,B,C,E]
Festuca idahoensis[B,C]		*Elaeagnus angustifolia*[A,E]
Festuca saximontana[B]		*Erodium cicutarium*[C,E]
Festuca thurberi[B]		*Erysimum cheiranthoides*[B,C]
Hesperostipa comata[A,B,C]		*Euphorbia agraria*[A]
Koeleria macrantha[A,B,C]		*Fallopia convolvulus*[C]
Leucopoa kingii[B,C]		*Festuca trachyphylla*[A]
Leymus ambiguus[C]		*Gypsophila paniculata*[B,C]
Muhlenbergia cuspidata[B]		*Lactuca serriola*[A,B,C]
Muhlenbergia montana[A,B,C]		*Linaria vulgaris*[B,C,E]
Nassella viridula[B]		*Malus sylvestris*[A]
Piptatherum micranthum[A,B,C]		*Matricaria discoidea*[C]
Pleuraphis jamesii[B]		*Medicago lupulina*[A]
Poa fendleriana[A,B,C]		*Myosotis alpestris*[A]
Poa interior[C]		*Myosotis scorpioides*[B]
Poa palustris[A]		*Onopordum acanthium*[C,E]
Poa sandbergii[B]		*Panicum miliaceum*[C,E]
Poa secunda[B]		*Poa compressa*[C]
Pseudoroegneria spicata[A,B]		*Poa pratensis*[A,B,C]
Schizachyrium scoparium[A,B,C]		*Polygonum aviculare*[C]
Sporobolus cryptandrus[A,B]		*Polygonum convolvulus*[C]
Sporobolus heterolepis[C]		*Raphanus sativus*[A]
Trisetum spicatum[B]		*Salsola tragus*[C,E]
Vulpia octoflora[A]		*Silene latifolia*[A]
		Sisymbrium altissimum[A,B,C]
		Taraxacum officinale[A,B,C]
		Tragopogon dubius[A,B,C]
		Trifolium pratense[C]
		Trifolium repens[A,B,C]
		Triticum aestivum[A]
		Ulmus pumila[A,E]
		Verbascum thapsus[A,B,C,E]
		Zea mays[A]

[A]Species found at the Cerro Grande Fire; [B]species found at the Hi Meadow Fire; [C]species found at the Hayman Fire; [D]seeded grasses that are non-native; [E]species classified as noxious in Colorado and/or New Mexico.