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Impacts of mixed severity wildfire on exotic plants in a Colorado ponderosa pine–Douglas-fir forest

Paula J. Fornwalt · Merrill R. Kaufmann · Thomas J. Stohlgren

Abstract The 2002 Hayman Fire burned with mixed severity across 55,800 ha of montane Colorado forest, including pre-existing plots that were originally measured for understory plant composition and cover in 1997. We examined the influence of the Hayman Fire on exotic plants by remeasuring these plots annually from 2003 to 2007. We found that (1) exotic richness and cover generally increased as fire severity and time since fire increased; (2) the exotic species present in a plot before the fire were also largely present in the plot postfire, regardless of fire severity; (3) most of the new postfire species in a plot were present elsewhere in the study area before the fire, although some new species were truly new invaders that were not found in prefire surveys; (4) lightly burned riparian forests were not more susceptible to exotic invasion than surrounding uplands that burned with similar severity; and (5) native and exotic richness and cover were positively correlated or uncorrelated for all fire severities and years. Our findings indicate that exotics were stimulated by the Hayman Fire, especially in severely burned areas. However, exotic richness and cover remain low as of 2007, and correlations between native and exotic richness and cover suggest that exotics have not yet interfered with native understory development. Therefore, we conclude that exotic plants are not a major ecological threat at present, but recommend that monitoring be continued to evaluate if they will pose a threat in future years.

Keywords Exotic plants · Fire severity · *Pinus ponderosa* · Riparian areas · Time since fire

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Introduction

Fire is a key ecological process in montane coniferous forests of the western United States, and it plays critical roles in regulating and sustaining native understory plant communities (Koniak 1985; Laughlin et al. 2004; Turner et al. 1999). However, fires can also facilitate the establishment and spread of exotic plant species (Zouhar et al. 2008). Given that the occurrence of fire in western forests—both wild and prescribed—has increased in recent decades and is likely to continue to increase in the future (USDOI

and USDA Forest Service 2009; Brown et al. 2004; Westerling et al. 2006), it is important that we develop a thorough understanding of the factors influencing postfire exotic plant response.

Fire characteristics such as fire severity often impact exotic plant establishment in burned coniferous forests. Exotics repeatedly have been found to be least stimulated in lightly burned forests where overstory tree mortality and forest floor consumption are minimal, and most stimulated in severely burned forests where tree crowns and forest floor are largely consumed (Crawford et al. 2001; Freeman et al. 2007; Hunter et al. 2006). The response of exotic plants after fire also often varies with time since fire (Klinger et al. 2006; Koniak 1985; Nelson et al. 2008). Additionally, there can be a significant interaction between fire severity and time since fire, as found by Keeley et al. (2003). They monitored postfire exotic response in Sierra Nevada forests one and three years after fire, and found that exotic richness and cover were not stimulated by low or high severity fire in the first postfire year, but in the third year, exotic richness and cover escalated in the high severity but not in the low severity sites.

Characteristics of the prefire plant community, such as the degree of prefire exotic invasion, can also shape exotic response after fire. For example, plant communities with a significant prefire exotic component due to a history of past human disturbance often become more heavily invaded after fire than those where a lack of human disturbance has kept exotic species at bay (Huisinga et al. 2005). Species-rich areas such as riparian corridors also tend to be hotspots of exotic invasion (Fornwalt et al. 2003; Stohlgren et al. 1999, 2005), and so they too may become considerably more invaded after fire. Similarly, the composition of the prefire exotic community is also important, as not all exotic species respond equally to fire. Where highly fire-adapted species are present in the prefire community, fire typically provides them with a foothold to expand (Dodge et al. 2008; Ferguson et al. 2007; Keeley and McGinnis 2007), while less adapted species may respond neutrally or even decline after fire (DiTomaso et al. 1999; Whisenant and Uresk 1990).

Exotic species can threaten native plant communities, and even drive localized native species extinctions in extreme cases (Alvarez and Cushman 2002; Minchinton et al. 2006; Walker and Vitousek 1991). Simple correlations between measures of native and exotic plant abundance (e.g., richness, cover, density) can provide insight into whether or not exotics are negatively impacting native species. If exotics are outcompeting natives, there would likely be a negative correlation between natives and exotics; on the other hand, a positive correlation may indicate that natives and exotics are responding similarly to environmental conditions. This approach has been employed by many researchers (Brown and Peet 2003; Parker et al. 1993; Stohlgren et al. 1999), although rarely in the context of fire (but see Keeley et al. 2003).

In 2002, the Hayman Fire, Colorado, burned across 55,800 ha of ponderosa pine–Douglas-fir (*Pinus ponderosa*–*Pseudotsuga menziesii*) forest (Graham 2003). Also burned in the fire were 25 pre-existing 1,000-m^2 plots that had been surveyed for understory plant composition and cover in 1997. These plots were located in both upland and riparian areas, and burned with a range of severities. We examined the short-term impacts of this fire on exotic plant communities by remeasuring the plots annually from 2003 to 2007. Specifically, we addressed the following questions:

1. How did fire severity and time since fire influence exotic richness and cover in burned forests?
2. Was there mainly a return of exotic species that were already present before the fire, or was there a true invasion of new species after fire?
3. Were riparian forests more vulnerable or less vulnerable to postfire exotic invasion than upland forests that burned with a similar severity?
4. Were native and exotic richness and cover correlated (either positively or negatively), and did fire severity or time since fire influence the strength or the direction of this correlation?

Methods

Study area and study design

We conducted our study in a 4 km^2 portion of the Pike National Forest, Colorado, USA, approximately 60 km southwest of Denver. Forests within the study area are dominated by ponderosa pine and Douglas-fir, and forest understories are a diverse assemblage of graminoids, forbs, and shrubs (Fornwalt et al. 2009; Kaufmann et al. 2000). Common graminoids

include prairie Junegrass (*Koeleria macrantha*) and mountain muhly (*Muhlenbergia montana*), while common forbs include yarrow (*Achillea millefolium*), nodding onion (*Allium cernuum*), and hairy false goldenaster (*Heterotheca villosa*). Wax currant (*Ribes cereum*) and kinnikinnick (*Arctostaphylos uva-ursi*) are common shrubs. Soils are well-drained gravelly coarse sandy loams derived from weathered Pikes Peak granite (USDA Forest Service 1992). Elevations within the study area range from 2,300 to 2,500 m. Precipitation averages 40 cm annually, most of which falls during the spring and summer (www.wrcc. dri.edu). January is the coldest month, with average highs of 7.3°C and average lows of −13.0°C; the warmest temperatures occur in July, when maximum daytime temperatures average 28.9°C (www.wrcc. dri.edu).

The study area and the plots within it were originally established and measured in 1996 and 1997 by Kaufmann et al. (2000). Five plots were established in each of five topographic environments, for a total of 25 plots: north-facing slopes, south-facing slopes, east- or west-facing slopes, ridgetops, and riparian areas. All plots were 1,000 m^2 (20 × 50 m) and were located in forested areas. North, south, and east/west plots were situated on upland slopes with the long axis of the plot aligned down the fall line. Ridgetop plots were also in upland areas, with the long axis parallel to the ridge. Riparian plots were located in low-lying valley bottoms or draws near intermittent or perennial streams, with the long axis of the plot parallel to the stream channel.

In 2002, the Hayman Fire burned 55,800 ha, including our study area (Graham 2003). Approximately half of the Hayman Fire area burned as a stand replacing crown fire, much of it in a single day of extreme weather. The other half burned as a mixed severity fire, creating a heterogeneous mosaic of burn severities on the landscape. Our study area is situated in a transitional zone between these two fire behaviors, and therefore contains components of each. In 2003, we successfully relocated and remeasured all of the original plots. Plots were also measured in 2004, 2005, 2006, and 2007.

Data collection

Understory data were collected using the modified-Whittaker sampling design (Stohlgren et al. 1995).

This method uses a primary 1,000-m^2 plot with several subplots nested within it. One 100-m^2 subplot is located in the center of the main plot, and two 10-m^2 subplots are located in diagonally opposite corners. Ten 1-m^2 subplots are distributed around the perimeter of the main plot and the 100-m^2 subplot. Vegetative cover of each understory plant species was ocularly estimated in the ten 1-m^2 subplots. Species presence was recorded for each of the 10-m^2 subplots, the 100-m^2 subplot, and the 1,000-m^2 plot. All graminoid, forb, and shrub species were included in the understory surveys, but tree species were not. Approximately 11% of the plant observations were identified only to genus, while 1% were not identified at all. Generic observations were generally limited to a small number of genera for which we did not attempt to distinguish individual species, either because hybridization is common (e.g., *Rosa*), or because species are difficult to determine when sampled outside peak phenological development (e.g., *Carex*, *Chenopodium*). Generic observations were included in our analyses, while unidentified observations were excluded. Nomenclature follows the USDA Plants Database (USDA 2008), although varieties and subspecies are not distinguished. We determined the nativity (native or exotic to the continental United States) using the *Flora of North America* and the USDA Plants Database (Flora of North America Editorial Committee 1993; USDA 2008). Nativity was determined for generic identifications only when the classification was appropriate for all species known to occur in montane Front Range forests. Voucher specimens are stored at the USDA Forest Service Rocky Mountain Research Station in Fort Collins, Colorado.

Plot attribute, overstory, and forest floor data were collected for each plot. Slope, aspect, and elevation were documented when the plots were established (Kaufmann et al. 2000). At this time, diameter at breast height, species, height, and live or dead status were also measured for all trees over 1.37 m tall (Kaufmann et al. 2000). Live or dead status was assessed again in 2003 and percent overstory mortality due to fire was calculated for every plot. In all years, percent cover of abiotic variables including litter, duff, and bare soil were ocularly estimated in the ten 1-m^2 subplots. Percent overstory canopy cover was also assessed in all postfire years using a spherical densiometer. Densiometer measurements

were systematically recorded at eight points in each plot and averaged. Prefire canopy cover measurements were not taken but were estimated using a linear regression of canopy cover versus the log of basal area, which was developed in Microsoft Excel 2003 (Microsoft Corporation, Redmond, Washington, USA) with a dataset collected in nearby unburned plots ($n = 44$; $p < 0.001$; $r^2 = 0.481$; PJ Fornwalt unpublished data).

Postfire rehabilitation treatment maps created by the USDA Forest Service indicate that four plots were aerially seeded in the fall of 2002. The seed used in the rehabilitation treatment was a certified weed-free mixture of 70 percent barley (*Hordeum vulgare*) and 30 percent triticale ($\times$*Triticosecale rimpaui*), and was applied at a rate of ~ 280 seeds m^{-2} (Robichaud et al. 2003). Both barley and triticale are exotic, non-persistent, annual grasses. Seeded grasses were most abundant in our plots in 2003, and were found in each of the four "seeded" plots, as well as in 10 of the 21 "unseeded" plots. However, even in 2003 seeded grass cover was negligible (<0.1%), although preliminary data analyses indicate that it was statistically greater in seeded than in unseeded plots ($p = 0.004$). In all other years, seeded grass cover did not differ between unseeded and seeded plots ($p = 1.000$). In light of these findings, we concluded that it was not necessary to analyze the seeded and unseeded plots separately in this study.

Statistical analyses

To aid in data analysis, plots were classified into groups that reflected their fire severity and topographic position. Plots where less than 50% of the overstory trees died in the Hayman Fire were categorized as having burned with low severity, while plots that burned with moderate severity had more than 50% mortality but did not experience much crown consumption. High severity plots were those with 100% overstory mortality and complete or nearly complete crown consumption. Topographic position was defined as either upland (i.e., north, south, east–west, and ridgetop) or riparian based on the plot's original topographic designation; previous work in these plots found few differences in prefire understory composition among upland categories, although upland plots differed considerably from riparian ones (Fornwalt et al. 2003, 2009). Prefire and

postfire overstory canopy cover and cover of forest floor components for low, moderate, and high severity upland plots and for low severity riparian plots are shown in Table 1. Moderate and high severity riparian plots are not included in this table or in any subsequent analyses because they are not sufficiently replicated. All prefire data were assigned a year of 1997 even though some plots were measured in 1996 because growing season precipitation and plant community composition did not differ between the two prefire years (Fornwalt et al. 2003, 2009).

We used repeated measures analysis of variance (ANOVA) in SAS 9.1.3 (SAS Institute, Cary, North Carolina, USA) to examine how time since fire, fire severity, and topographic position influenced several exotic metrics. The metric *total exotic richness* was calculated by tallying the number of exotic species in each 1,000-m^2 plot. Total exotic richness was further divided into the *richness of legacy exotic species* and the *richness of new exotic species*. Legacy species were those found in a plot's pre-Hayman survey, while new exotic species were those found in a plot only after the fire. An exotic species could be a legacy species in one plot but a new species in another depending on whether or not it was recorded in the prefire survey. *Total exotic cover* per 1,000-m^2 plot was calculated by summing the cover of all exotic species in each 1-m^2 subplot and averaging across all subplots. We first analyzed the impact of time since fire and fire severity on exotic response in upland areas by separately modeling each of the four dependent exotic variables described above against the independent variables year, fire severity, and year $\times$ fire severity. We then analyzed the impact of time since fire on exotic response in low severity riparian areas by modeling each exotic variable against year. Finally, we compared low severity riparian and low severity upland areas by modeling total exotic richness and cover against year, topographic position, and year $\times$ topographic position. All of these repeated measures analyses used the spatial power covariance matrix, which assumes that there is a higher level of correlation between two repeated observations closer in time than between two observations further apart. Nonsignificant independent variables ($p \geq 0.05$) were iteratively excluded until only significant variables remained. Significant variables were further examined for

Table 1 Mean prefire (1997) and postfire (2003–2007) percent cover of overstory and forest floor components (±SE), by fire severity and topographic category

Year	Overstory Canopy cover[b]	Forest floor[a] Understory cover[c]	Litter cover	Bare soil cover
Upland, low severity fire ($n = 10$; overstory mortality = 21%)				
Prefire	51.0 ± 2.3	19.7 ± 2.6	48.2 ± 1.9	30.2 ± 1.8
Postfire	52.6 ± 4.2	15.6 ± 2.5	39.5 ± 2.8	41.8 ± 3.1
Upland, moderate severity fire ($n = 6$; overstory mortality = 67%)				
Prefire	56.9 ± 1.1	23.6 ± 4.1	63.4 ± 4.3	13.7 ± 2.9
Postfire	42.5 ± 5.2	20.0 ± 5.1	41.6 ± 5.0	33.1 ± 4.0
Upland, high severity fire ($n = 4$; overstory mortality = 100%)				
Prefire	52.8 ± 5.4	17.6 ± 2.4	54.4 ± 2.3	21.2 ± 4.8
Postfire	23.6 ± 4.9	19.0 ± 6.4	5.5 ± 1.8	71.7 ± 6.3
Riparian, low severity fire ($n = 4$; overstory mortality = 33%)				
Prefire	56.7 ± 3.0	44.1 ± 11.6	53.0 ± 6.2	11.8 ± 4.3
Postfire	68.8 ± 8.0	32.9 ± 7.0	42.4 ± 7.1	21.9 ± 6.4

[a] The sum of the forest floor variables may exceed 100% because of overlap among the elements

[b] Overstory canopy cover is contributed by tree foliage, stems, and branches. Prefire canopy cover was approximated using a linear regression of canopy cover versus the log of basal area, which was developed with a dataset collected in nearby unburned plots ($n = 44$; $p < 0.001$; $r^2 = 0.481$; PJ Fornwalt unpublished data)

[c] Understory cover includes all understory plant species (native + exotic)

pairwise differences between variable levels using least squares means with a Tukey–Kramer adjustment for multiple comparisons. Cover data were square-root transformed to approximate ANOVA assumptions of residual normality and homoscedasticity; otherwise, no serious violations of ANOVA assumptions were encountered.

We also determined the correlation between total exotic and total native richness and cover. Our approach was twofold. First, we used repeated measures ANOVAs to determine whether year and/or fire severity interacted with the relationship between exotics and natives. Two separate ANOVA models were constructed: we modeled total native richness against total exotic richness, year, fire severity, total exotic richness × year, total exotic richness × fire severity, and total exotic richness × year × fire severity, and we modeled total native cover against total exotic cover, year, fire severity, total exotic cover × year, total exotic cover × fire severity, and total exotic cover × year × fire severity. Upland and riparian plots were combined for these analyses. Nonsignificant ($p \geq 0.05$) variables were iteratively excluded from the models as before. Second, if significant year and/or fire severity interactions were found, we partitioned the

data as appropriate and constructed separate linear regressions for each level of year and/or fire severity. For example, if total exotic cover × year was a significant predictor of total native cover, we partitioned the data by year and conducted separate linear regressions of total native cover versus total exotic cover for each year. Again, cover variables were square-root transformed prior to analysis.

Results

We identified 21 exotic plant species over the 6 years of this study (Table 2), accounting for 8.5% of all understory species found. Ten of these species are annual, biennial, or short-lived perennial forbs; we also found three perennial forbs, three annual graminoids, and five perennial graminoids. Five of the exotic species are noxious weeds in the state of Colorado: cheatgrass (*Bromus tectorum*), musk thistle (*Carduus nutans*), Canada thistle (*Cirsium arvense*), butter and eggs (*Linaria vulgaris*), and common mullein (*Verbascum thapsus*).

Common mullein was the most widespread exotic species; when averaged over all years it was found in

Table 2 Exotic species documented before and after the 2002 Hayman Fire, and percent of 1,000-m^2 plots containing each exotic species, by year

Species	Growth form[a]	Percent of plots ($n = 24$)					
		1997	2003	2004	2005	2006	2007
Agropyron cristatum, crested wheatgrass	P graminoid	0	0	8	0	0	0
Axyris amaranthoides, Russian pigweed	A forb	0	13	4	0	0	0
Bassia scoparia, burningbush	A forb	4	0	0	0	0	0
Bromus inermis, smooth brome	P graminoid	13	13	13	21	17	25
Bromus tectorum, cheatgrass[b]	A graminoid	0	0	0	0	0	21
Camelina microcarpa, littlepod false flax	A/B forb	0	4	4	0	0	0
Carduus nutans, musk thistle[b]	B/P forb	4	0	13	21	38	33
Cirsium arvense, Canada thistle[b]	P forb	4	38	33	33	38	50
Dactylis glomerata, orchardgrass	P graminoid	0	4	0	0	0	0
Descurainia sophia, herb sophia	A/B forb	0	0	0	4	4	4
Lactuca serriola, prickly lettuce	A/B forb	0	58	54	79	58	88
Linaria vulgaris, butter and eggs[b]	P forb	13	13	46	25	29	21
Phleum pratense, timothy	P graminoid	0	0	4	0	4	4
Poa annua, annual bluegrass	A graminoid	4	0	0	0	0	0
Poa pratensis, Kentucky bluegrass	P graminoid	25	17	17	17	17	17
Polygonum convolvulus, black bindweed	A forb	0	4	0	0	0	0
Sonchus asper, spiny sowthistle	A forb	0	0	4	0	0	0
Taraxacum officinale, common dandelion	P forb	50	38	50	63	83	88
Tragopogon dubius, yellow salsify	A/B forb	13	8	38	54	54	79
×*Triticosecale rimpaui,* triticale	A graminoid	0	54	29	50	4	8
Verbascum thapsus, common mullein[b]	B forb	38	79	92	96	83	100

[a] Growth form was determined using the USDA Plants Database (USDA 2008) and local botanical keys. *A* annual, *B* biennial, *P* perennial

[b] This species is classified as a noxious weed by the state of Colorado

81% of plots (Table 2). The two next most widespread species, common dandelion (*Taraxacum officinale*) and prickly lettuce (*Lactuca serriola*), were found in an average of 62 and 56% of plots, respectively (Table 2). All other exotic species occurred in less than 50% of plots on average. Common mullein also had the greatest cover of any exotic species, averaging 0.3% cover across all plots and years and accounting for over 40% of total exotic cover. Kentucky bluegrass (*Poa pratensis*) and common dandelion were the next most abundant species in terms of cover, averaging 0.1% cover each. Cover of all other exotics averaged < 0.1% each.

Exotic richness and cover in upland sites

Prior to the 2002 Hayman Fire, upland plots contained an average of 1.1 exotic species per 1,000-m^2 plot, whereas after the fire, they contained an average of 3.8 species. Total exotic richness was related to year ($p < 0.001$), fire severity ($p = 0.002$), and year × fire severity ($p < 0.001$). In low severity plots, total exotic richness after fire increased relative to prefire levels only in 2007, but in moderate and high severity plots, total exotic richness was greater after fire than before in four of the five postfire years (Fig. 1a). Furthermore, total exotic richness after fire in moderate and high severity plots generally increased as time since fire passed, although not always significantly so. Comparing fire severities, we found that total exotic richness did not differ between low, moderate, and high severity plots in 1997, 2003, or 2004, but from 2005 to 2007, total richness of exotic species in moderate and high severity areas was nearly always greater than in low severity areas (Fig. 1a).

Fig. 1 Mean and SEs for exotic richness in upland plots, by year and fire severity. The bars in (**a**) are shaded to reflect the relative contributions of legacy (*black*) and new (*grey*) exotic species to total exotic richness. Legacy species are those species that were found in an individual plot before the fire, while new species are species that were not present in a plot before the fire but were present after the fire. *Different letters* indicate significant differences in richness among years for an individual fire severity class ($p < 0.050$)
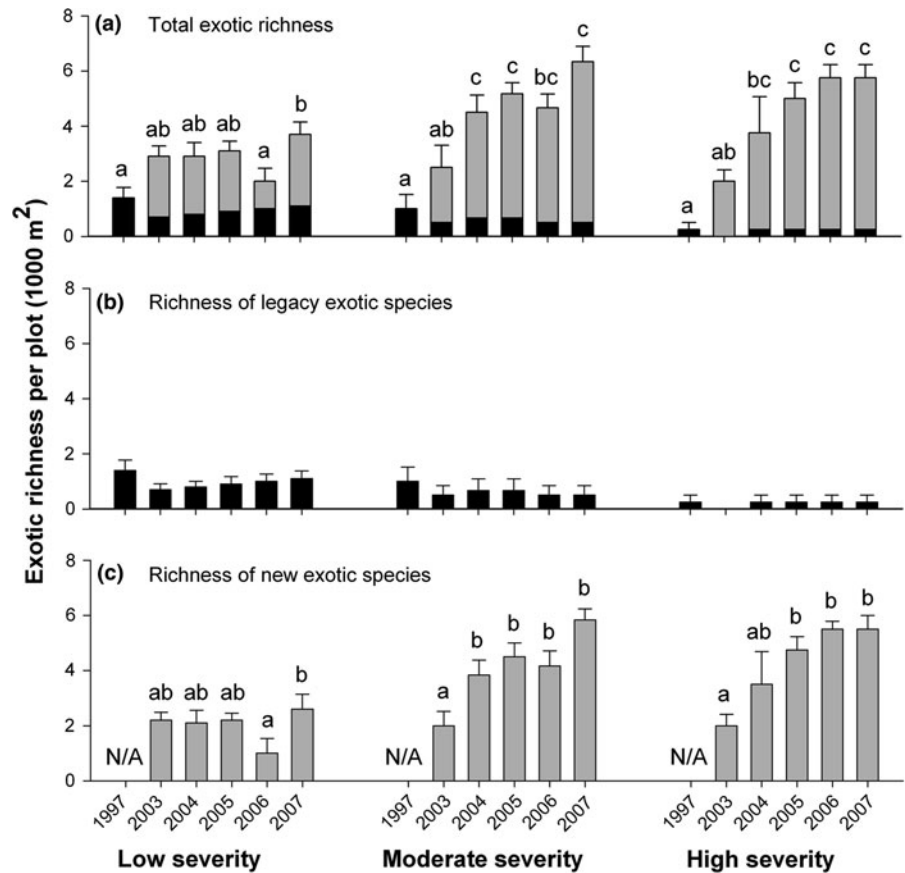
On average, 18% of the exotics occurring in postfire plots were legacy species originally found in the plot's prefire survey, while 82% were new species not previously found. Richness of exotic legacy species was not related to year ($p = 0.358$), fire severity ($p = 0.233$), or year × fire severity ($p = 0.991$), indicating that postfire plots contained most of the species originally found before the fire, regardless of time since fire or fire severity (Fig. 1b). However, the richness of new exotic species per plot was related to year ($p < 0.001$), fire severity ($p < 0.001$), and year × fire severity ($p = 0.002$), with postfire trends through time and among fire severities closely following the trends observed for total exotic richness (Fig. 1c).

Total exotic cover in upland areas averaged <0.1% prior to the Hayman Fire. Total exotic cover increased postfire, although it only averaged 0.5% across all years and fire severities. As with total exotic richness, total exotic cover was significantly related to year ($p < 0.001$), fire severity ($p = 0.017$), and year × fire severity ($p = 0.010$). In lightly burned areas, total exotic cover after fire never varied from prefire cover, but in moderately and severely burned areas, a postfire increase was apparent in one or more years (Fig. 2). Total exotic cover did not differ among fire severities in 1997, 2003, or 2004, but was greater in moderate and/or high severity plots than in low severity plots from 2005 through 2007.

Exotic richness and cover in lightly burned riparian areas

Neither total exotic richness nor total exotic cover in low severity riparian plots varied over time ($p = 0.522$ and 0.296, respectively); across all years, the exotic community in these plots averaged 6.6 species and 1.6% cover. Fifty-five percent of the postfire exotic species in a plot were legacy species, while 45% were new species not previously found. The richness of legacy and new exotic species also did not vary over time ($p = 0.707$ and 0.843,

Fig. 2 Mean and SEs for total exotic cover in upland plots, by year and fire severity. *Different letters* indicate significant differences among years for an individual fire severity class ($p < 0.050$)
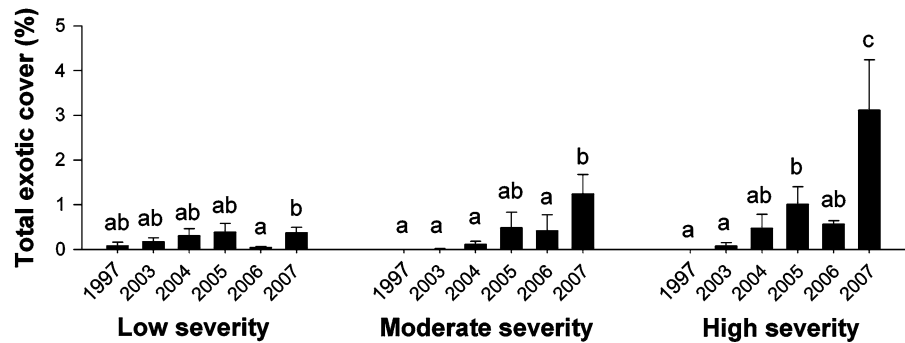
respectively). Relative to lightly burned upland plots, lightly burned riparian plots had greater total exotic richness and cover over the course of the study (topographic category: $p < 0.001$ and $p = 0.003$, respectively), although trends through time for the two topographic positions were similar (year $\times$ topographic category: $p = 0.097$ and 0.286, respectively).

Correlations between natives and exotics

Total native richness was related to total exotic richness ($p = 0.002$), year ($p < 0.001$), and total exotic richness $\times$ fire severity ($p = 0.005$), but not to fire severity, total exotic richness $\times$ year, or total exotic richness $\times$ year $\times$ fire severity ($p = 0.301$, 0.498, and 0.105, respectively). The relationship between total native and total exotic richness was positive and significant for all fire severities (Fig. 3a, c).

Total native cover was related to total exotic cover ($p = 0.003$), year ($p < 0.001$), and total exotic cover $\times$ year ($p = 0.025$), but not to fire severity, total exotic cover $\times$ fire severity, or total exotic

cover $\times$ year $\times$ fire severity ($p = 0.507$, 0.829 and 0.531, respectively). Total native and total exotic cover were significantly and positively correlated in 1997, 2003, 2004, 2006, and 2007 (Fig. 4a–d, f), and non-significantly but positively correlated in 2005 (Fig. 4e).

Discussion

Impacts of fire severity and time since fire on exotic species in uplands

Total exotic richness and cover in uplands were highly dependent on fire severity (Figs. 1a, 2), with exotics being least stimulated by fire in lightly burned areas where less than 50% of the forest overstory was killed, and most stimulated in moderately and severely burned areas where overstory mortality exceeded 50%. Our findings are consistent with a growing body of research on exotic invasions in recently burned ponderosa pine forests.
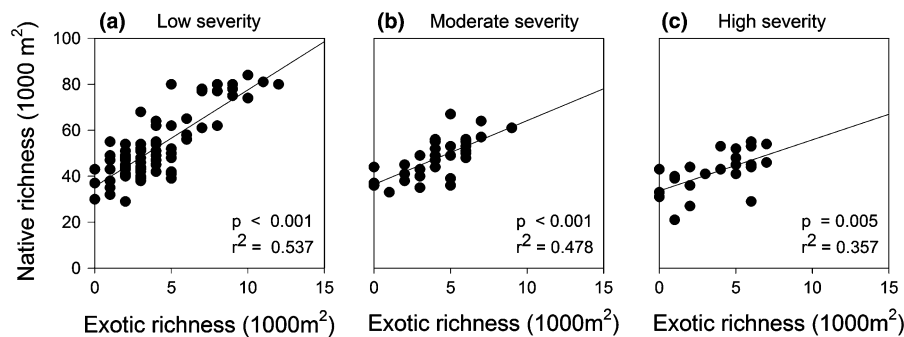

Fig. 3 Scatterplots depicting the relationship between native and exotic richness in 1,000-m^2 plots, by fire severity. Data were combined across all years because the interaction terms total exotic richness $\times$ year and total exotic richness $\times$ year $\times$ fire severity were not significant in the model

Fig. 4 Scatterplots depicting the relationship between native and exotic cover, by year. The *axes* are on a square root scale so that the untransformed cover values could be presented. Data were combined across all fire severities because the interaction terms total exotic richness × fire severity and total exotic richness × year × fire severity were not significant in the model
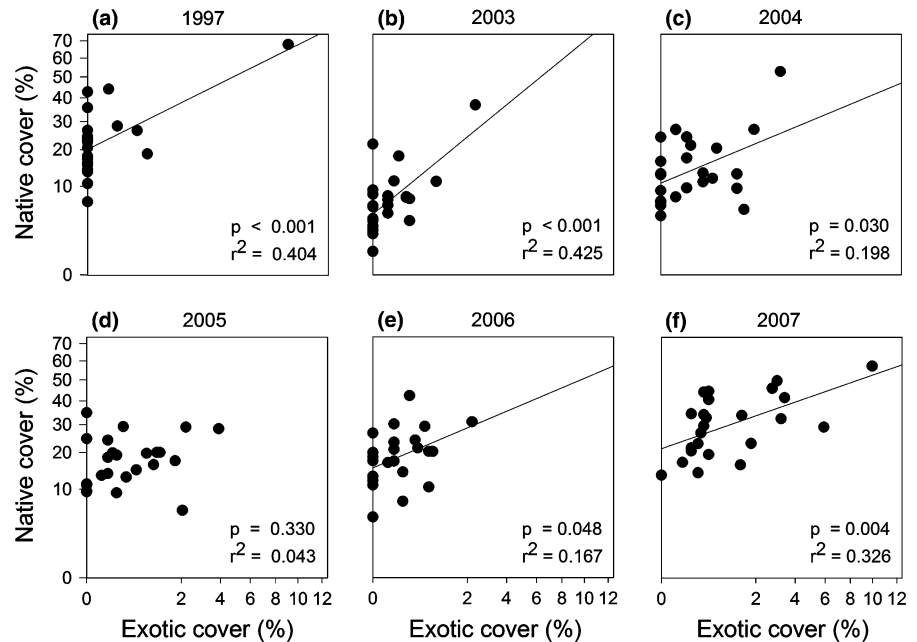
For example, Crawford et al. (2001) document a dramatic increase in exotic cover with increasing burn severity following three Arizona wildfires. They found that exotic cover jumped from 0% in nearby unburned stands to 59% in moderately burned stands and 116% in severely burned stands. [Note that the cover of Canadian horseweed (*Conyza canadensis*), which is considered native by the authority we used (USDA 2008), equals 27% and 18% in moderately and severely burned stands, respectively.] Freeman et al. (2007) found more moderate influences of fire severity; in their study of seven wildfires, exotic cover ranged from ∼1% in unburned stands to ∼2% in lightly burned stands and ∼3% in severely burned stands, which is comparable to the findings presented here. Mechanisms to explain exotic response to fire have been repeatedly linked to the postfire availability of resources such as light and bare soil, which are critical for exotic establishment and growth (Freeman et al. 2007; Keeley et al. 2003). Our lightly burned stands had nearly twice the canopy cover and half the exposed soil cover as severely burned stands (Table 1), suggesting that these resources are also important drivers of exotic response in this system.

Most studies on exotic response after mixed severity wildfire are conducted for only 1 or 2 years, so little is known about longer-term dynamics. Although exotic plant richness and cover in our

study area were low for all years, even in the most heavily invaded locations, our data show that exotics tended to become increasingly more abundant in moderately and severely burned sites as time since fire passed. In contrast, exotics in lightly burned areas changed little over the course of the study (Figs. 1a, 2). Again, abundant levels of light and bare soil probably explain much of these postfire temporal patterns; even 5 years after fire, severely burned forests still had nearly 60% bare soil cover, and overstory canopy cover (from dead tree branches) was only 17% (data not shown). Annual variability in precipitation may also be driving temporal patterns to some extent (Keeley et al. 2005), although postfire precipitation was below the average of 40 cm year^{-1} in all years (range: 19 cm year^{-1} in 2003 to 36 cm year^{-1} in 2006; www.wrcc.dri.edu).

The dearth of long-term research on exotic plant response after mixed severity wildfire makes it difficult to predict how exotics in the Hayman Fire will behave in the future. Other factors that also influence exotic abundance, such as development within the wildland-urban interface, forest management activities, and climate change, further complicate predictions (Heckmann et al. 2008; Keeley 2006; Thuiller et al. 2007). That being said, our data suggest that the level of invasion in lightly burned areas of the Hayman Fire will remain relatively unchanged in the

foreseeable future. However, exotics may continue to expand in areas where the Hayman Fire burned hottest. Continued monitoring of exotic species within mixed severity wildfires such as the Hayman is needed if long-term patterns of postfire exotic invasion are to be better understood.

The importance of "legacy" and "new" species in postfire exotic invasions

Our prefire dataset provides unique evidence that prefire exotic community composition at both local (i.e., plot) and landscape (i.e., study area) scales strongly influences the postfire exotic community that develops at a given location. We found that, regardless of fire severity and topographic position, the exotic species that were present in a plot before the fire were also largely present in the plot after the fire (Fig. 2a). Only two species found in the prefire survey, burningbush (*Bassia scoparia*) and annual bluegrass (*Poa annua*), were never found in postfire surveys (Table 2), and these species were only found in one prefire plot each. The high rate of exotic return is likely because many of the prefire exotic species are perennials that are able to rapidly reestablish after disturbance by sprouting from surviving underground parts. For example, smooth brome (*Bromus inermis*), Canada thistle, and Kentucky bluegrass have all been observed to sprout after fire (Stickney and Campbell 2000; USDA Forest Service 2008; Willson and Stubbendieck 1997), and the morphology of butter and eggs and common dandelion suggests that they can sprout as well.

Furthermore, most new exotic species in a plot were present elsewhere in the study area before the fire (Table 2). Many of the most aggressively spreading of these species have seeds which are capable of being dispersed long distances by wind, such as the noxious weeds musk thistle (*Carduus nutans*) and Canada thistle (Smith and Kok 1984; USDA Forest Service 2008; Wood and del Moral 2000). An exception to this was the noxious weed common mullein, which was found in 38% of plots before the Hayman Fire and 100% of plots 5 years after fire (Table 2). Common mullein seeds typically fall to the ground in the vicinity of the parent plant and enter the soil seedbank (Gross and Werner 1978). Seeds of common mullein can persist in the soil for decades (Kivilaan and Bandurski 1981), thereby

enabling it to reestablish in areas long after it has disappeared from the aboveground plant community. Postfire expansion of musk thistle, Canada thistle, and common mullein populations has been documented throughout the western United States (Crawford et al. 2001; Doyle et al. 1998; Floyd et al. 2006; USDA Forest Service 2008).

However, some new exotic species were truly new invaders that were not found in any prefire surveys (Table 2). The most notable of these are prickly lettuce (*Lactuca serriola*), triticale (×*Triticosecale rimpauii*) and cheatgrass (*Bromus tectorum*). While prickly lettuce likely established via long-distance seed dispersal (Weaver and Downs 2003), triticale and cheatgrass are known to have been introduced during postfire rehabilitation activities. Triticale was intentionally seeded to help stabilize the soil (Robichaud et al. 2003); in contrast, cheatgrass was unintentionally dispersed as a contaminant of straw mulch (Chong et al. 2003). Contaminated rehabilitation materials have also been inadvertently used on other wildfires, such as the 2000 Cerro Grande Fire in New Mexico (Keeley et al. 2006). The arrival of cheatgrass within the Hayman perimeter is particularly disturbing, as it is an aggressive invader that can rapidly establish and spread after fire (Floyd et al. 2006). Indeed, some areas of the Hayman Fire that were mulched with straw have become heavily infested with cheatgrass (PR Robichaud and JW Wagenbrenner, unpublished data), and our data suggest that cheatgrass may be beginning to expand to unrehabilitated areas as well. Heavy cheatgrass establishment often has dire ecological consequences, such as increased fuel production and fire frequency and decreased native species diversity (Knapp 1996).

Exotic invasion in lightly burned riparian areas

Riparian areas are often hotspots of exotic plant invasion in unburned forests (DeFerrari and Naiman 1994; Stohlgren et al. 1999, 2005). In fact, our prefire data show that unburned riparian areas in Colorado ponderosa pine forests may contain more than twice as many exotic species as the surrounding uplands (see also Fornwalt et al. 2003). Given the affinity of exotic species for riparian habitats, we expected that these areas would become heavily invaded after fire, yet we saw no significant change in exotic richness and cover during any of the five postfire years. While

riparian areas contained greater exotic richness and cover than uplands both before and after the fire, the insignificant interaction term year × topographic category indicates that trends through time were similar for lightly burned upland and riparian areas. This suggests that lightly burned riparian areas were not any more susceptible to exotic invasion after fire than surrounding upland forests that burned with a similar severity. It is important to reiterate that our riparian analyses are limited to lightly burned areas only, because an insufficient number of our prefire riparian plots happened to fall within areas of greater fire severity to provide adequate sample sizes. Clearly, more work is needed to untangle the relationship between fire severity and time since fire in these very sensitive and important ecosystems.

Correlations between native and exotic richness and cover

The positive or non-significant correlations we observed between native and exotic richness and cover suggest that exotic species have not yet impacted the recovering native plant community. While simple correlations such as this do not prove a cause-and-effect relationship between exotics and natives, the relatively low richness and cover of exotics and the ample amount of bare soil available for both native and exotic plant establishment provide support for our interpretation. Instead, our results suggest that conditions favorable for native species are also favorable for exotics, a phenomenon that has been well-documented in observational studies conducted in a variety of disturbed and undisturbed systems and across multiple spatial scales (Brown and Peet 2003; Keeley et al. 2003; Stohlgren et al. 1999).

Conclusions

Exotic species were favored by the 2002 Hayman Fire, especially in the most severely burned areas. However, exotic richness and cover remain low at this point in time, and native and exotic richness and cover remain positively or non-significantly correlated, so we do not consider them a major ecological threat at present. Continued monitoring is necessary to evaluate if exotics will pose a threat in future

years. Although other portions of the Hayman Fire may be more invaded than our study area—for example, along roads, in severely burned riparian areas, and in areas that were rehabilitated after the fire—we suspect that our findings are representative of much of the burn.

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