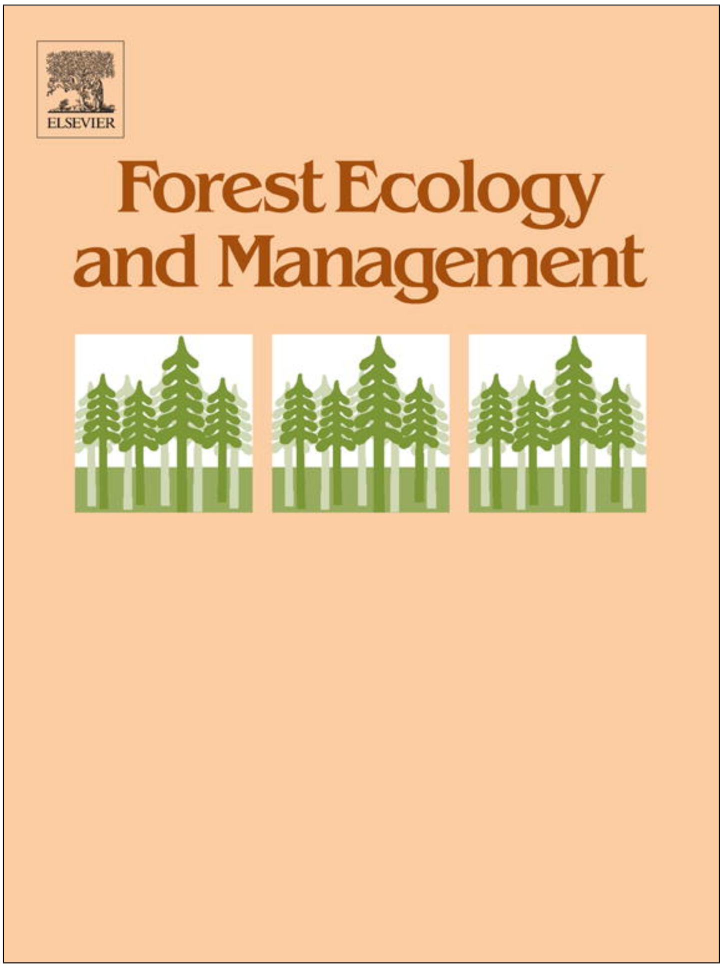
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Nonnative species influence vegetative response to ecological restoration: Two forests with divergent restoration outcomes

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ABSTRACT

Changes in the vegetative structure and diversity of ponderosa pine forests have generated interest in conducting ecological restoration projects to improve the overall forest health of these ecosystems. Ecological restoration prescriptions often consist of thinning trees to emulate pre-1870s forest structure followed by prescribed burning. Disturbances associated with ecological restoration can, however, promote invasion by nonnative species. We compared two northern Arizona ponderosa pine forests treated for ecological restoration, one at the Fort Valley Experimental Forest and one at Mt. Trumbull on the Grand Canyon-Parashant National Monument. We examined the response of native and nonnative plant species, as well as all species combined, to treatments at the two forests. Both study sites showed a significant increase in native and nonnative species cover and richness by the fifth year post-treatment that remained significant by the tenth year post-treatment. Despite these general trends in native and nonnative community development, the understory vegetation at the two sites followed diverging successional patterns after treatment. By the tenth year post-treatment Fort Valley was dominated by native species and Mt. Trumbull was dominated by a single nonnative species, cheatgrass. The differences in post-treatment understory recovery are likely due to pretreatment forest conditions. At Fort Valley, nonnatives were present, but accounted for only 0.11% of the pretreatment cover. At Mt. Trumbull, nonnatives accounted for 5.26% of the pretreatment understory cover, with cheatgrass accounting for approximately 4% of the understory cover. Additionally, the soil seedbank at Fort Valley had greater overall species richness and greater native perennial grass richness than Mt. Trumbull. We propose that the application of ecological restoration treatments should be targeted to sites with low abundance of nonnatives prior to treatment. Sites containing high abundance of nonnatives prior to treatment should be managed for nonnative species mitigation before initiating any ecological restoration projects.

1. Introduction

A century ago, the plant community of southwestern ponderosa pine forests consisted of fewer trees and greater understory diversity (Weaver, 1951; Cooper, 1960; Covington and Moore, 1994; Bakker and Moore, 2007; Laughlin et al., 2011). With the advent of Euro-American settlement in the region, fire suppression, extensive livestock grazing, and commercial logging practices altered the successional trajectory in favor of more trees and reduced understory. Contemporary southwestern ponderosa pine forests often contain dense, interconnected canopies with thick forest floor litter and duff layers. The commensurate shading and lack of bare mineral soil for seed germination has resulted in forests generally depauperate of understory vegetation (Covington and Moore, 1994; Laughlin et al., 2011). The disjunction between current and historical conditions in southwestern ponderosa pine forests has generated interest in using ecological restoration techniques to improve overall forest health and increase biodiversity (Covington et al., 1997; Moore et al., 1999). A common ecological restoration prescription in southwestern ponderosa pine forests is to thin trees to emulate historical forest structure from a time period pre-dating the disruption of the past disturbance regime, then reintroduce fire to the system (Covington and Moore, 1994; Moore et al., 1999).

Ecological restoration treatments consisting of tree removal and prescribed fire intentionally generate ecological disturbances. Tree thinning perturbs the soil and increases light infiltration to the understory, while prescribed fire removes much of the understory aboveground biomass, alters short-term nutrient cycling, and

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consumes accumulated litter and duff layers from the forest floor (Covington et al., 1997; DeLuca and Zouhar, 2000; Johnson and Curtis, 2001; Selmants et al., 2008). The ecosystem changes generated by restoration-induced disturbances promote increased growth and diversity in the native vegetative community (Moore et al., 2006). Disturbances associated with ecological restoration treatments can, however, have the unintended consequence of exposing the ecosystem to greater risk of invasion by undesired and detrimental nonnatives (Hobbs and Huenneke, 1992; Crawford et al., 2001; Griffis et al., 2001; Allen et al., 2002). While the presence of nonnatives is contrary to the objectives of ecological restoration (SER, 2004), an elevated presence of nonnatives in response to thinning and burning treatments is common (Wienk et al., 2004; Dodson and Fiedler, 2006; Moore et al., 2006; Nelson et al., 2008; Sabo et al., 2009). The risk of nonnative invasion has raised concerns regarding the utility of historical reference conditions as a standard protocol for designing ecological restoration treatments (Allen et al., 2002; D'Antonio and Meyerson, 2002; Noss et al., 2006; Hobbs et al., 2009; Jackson and Hobbs, 2009).

In this study we examined ecological restoration treatments in two ponderosa pine forests in northern Arizona, USA. The first study site is in the Uinkaret Mountains north of the Grand Canyon and the second is near the city of Flagstaff. Ecological restoration treatments were based on historical reconstruction of the overstory density and distribution combined with the application of prescribed fire. For both studies we have at least 10 years of post-treatment data collected with the same experimental design and methodology. We hypothesize that (1) the native understory will increase in cover and species richness in response to ecological restoration, (2) nonnatives will also increase in response to ecological restoration, and (3) the understory response to ecological restoration will be consistent in both study sites.

2. Methods

2.1. Study sites

The Fort Valley site is located in and adjacent to the Fort Valley Experimental Forest, approximately 15 km northwest of Flagstaff, AZ in the Coconino National Forest (35°16′19″N, 111°41′22″W). Elevation of the study area is approximately 2250 m. Mean annual precipitation during the duration of the sampling period (1997–2011) was 45 cm (Western Regional Climate Center, http://www.wrcc.dri.edu). Soils consist of fine, smectitic, frigid Mollisols and Alfisols derived from basaltic parent materials (Stoddard et al., 2011). Vegetation at this site is dominated by ponderosa pine, consisting of groups of mature trees intermixed with numerous dense thickets of smaller diameter trees. Prior to treatment, total trees per hectare averaged approximately 1188 and 901, respectively, in the control and treated units. In 1999, after both thinning and burning, tree density decreased by 0.1% and 84%, respectively, in the control and treated units (Korb et al., 2007). The site has not been actively grazed by cattle since the establishment of the Fort Valley Experimental Forest in 1909. The treated units were not seeded after burning except for a portion of each slash pile that was used in a slash pile amelioration study (Korb et al., 2004).

The Mt. Trumbull site is in the Grand Canyon-Parashant National Monument (GCPNM), located in the Uinkaret Mountains (36°22′N, 113°7′W). GCPNM is co-managed by the Bureau of Land Management and National Park Service. Elevation of the study area is approximately 2150 m. Mean annual precipitation during the duration of the sampling period (1997–2010) was 36 cm (Western Regional Climate Center, http://www.wrcc.dri.edu). Soils consist of shallow, cindery Inceptisols derived from basaltic parent materials (McGlone et al., 2009b). Vegetation at this site is dominated by ponderosa pine and Gambel oak (*Quercus gambelii*). Prior to treatments, total trees per hectare averaged approximately 1372 and 1375 respectively in the control and treated units. In 2000, after both thinning and burning, tree density decreased by 7% and 75% in the control and treated units (Fulé et al., 2007). The site is grazed from July 1 to October 31 by a maximum of 88 head for a total of approximately 300 AUMs for an average of 0.18 AUMs ha^{-1}. Cattle were excluded from the site between 1998 and 2002. The treated units were not seeded after burning.

2.2. Experimental design and treatments

The same experimental design was implemented at both Fort Valley and Mt. Trumbull. Treated units received a historical evidence-based ecological restoration treatment that included both thinning and prescribed fire. Tree thinning was based on site-specific reconstructions of pre-1870s forest structure using principles described by Moore et al. (1999). For each site, evidence of old-growth individuals (trees established prior to Euro-American settlement of the region in 1870) was used as a basis for live tree retention. In addition to retaining all old-growth trees, 1.5–3 additional trees were retained as replacement per old-growth individual evidence (e.g. logs, snags, and stumps from trees established prior to the 1870s). This procedure was designed to leave 150–300% of the trees per hectare we estimated existing in our pre-1870s forest structure reconstruction. The retention of more trees per hectare than levels determined by forest reconstruction offset potential errors in reconstructions and unpredicted mortality after treatment. The number of younger replacement trees depended on tree size. If the replacement trees were <40.6 cm diameter at breast height, the higher retention rate was used. In addition, trees in close proximity to each piece of evidence were preferentially retained to more closely approximate the pre-1870s spatial pattern. Prescribed fire was applied by drip torch using strip head fires. Additionally, each treated unit was paired with a control unit that was neither thinned nor burned.

Fort Valley contains three replicated experimental blocks and Mt. Trumbull contains four experimental blocks. Each experimental block contained two treatment units that were randomly assigned as either a treated or a control unit. Treatment units ranged in size from 14 to 16 ha, and each contained twenty 400 m^2 (11.28 m radius) fixed area monitoring plots established on a 60 m × 60 m grid. Plot centers were permanently marked with iron stakes to ensure exact relocation for sampling in subsequent years. Sampling protocol for herbaceous vegetation was modified from the National Park Service fire monitoring protocol (USDI NPS, 1992). Each plot included one 50 m point-line intercept transect oriented parallel to the prevailing slope and centered on plot center. Sampling points were located every 30 cm along each transect for a total of 166 points per plot. Species information was recorded any time a portion of a plant's live aboveground biomass intersected a sampling point. Species presence/absence was also record within a 10 m × 50 m (500 m^2) belt transect centered on the point-line intercept transect. Taxonomic nomenclature and species nativity follow the USDA Plants Database (USDA NRCS, 2012).

Tree thinning was conducted in 1999 at both sites except for one experimental block at Mt. Trumbull that was thinned in 1998. All blocks at both sites were initially burned in spring 2001 except for one experimental block at Fort Valley that was burned in spring 2000. All blocks at both sites were reburned in fall 2007. All pretreatment data were collected in 1998. We collected data in the first growing season post-treatment in summer 2001 at both sites except for the experimental block at Fort Valley that was burned in spring 2000 where we collected data in summer

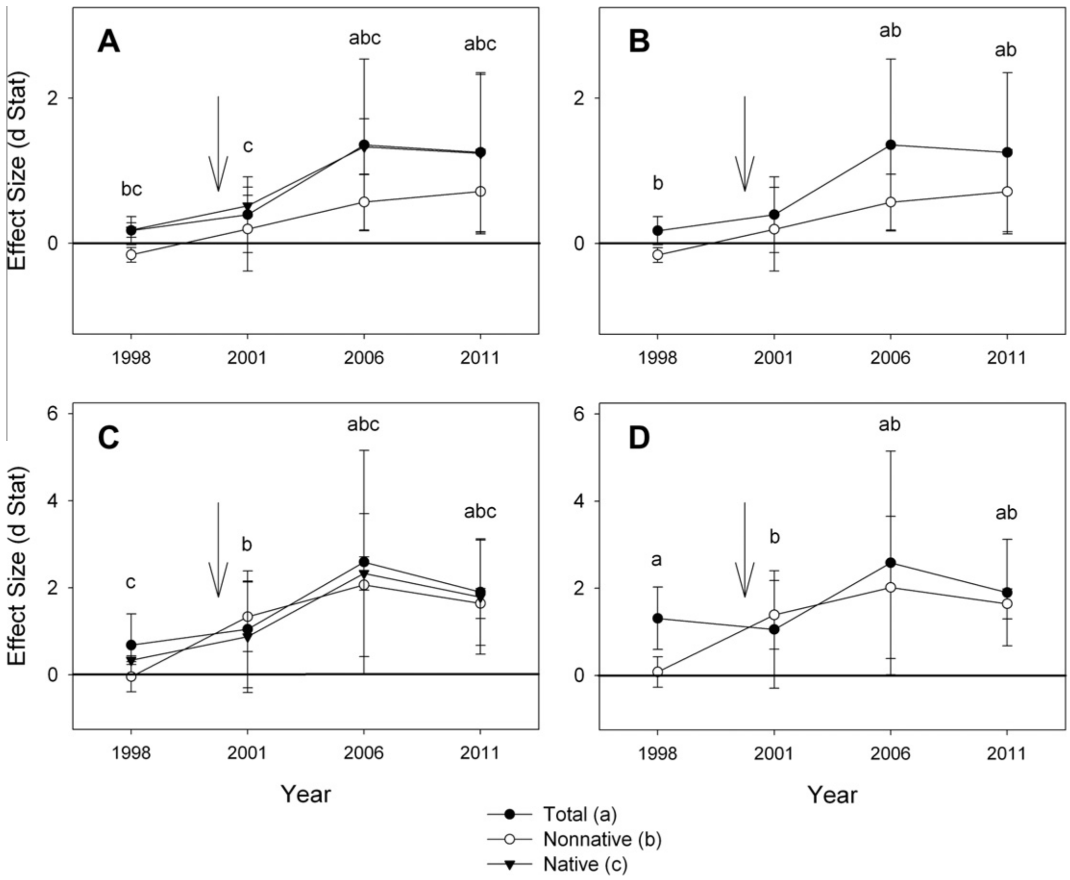

Fig. 1. Effect size results for the Fort Valley study site. Top panels show cover including cheatgrass (A) and excluding cheatgrass (B). Bottom panels show richness including cheatgrass (C) and excluding cheatgrass (D). Error bars show 95% CI. If symbol is above the zero line, magnitude of response was greater in treated units than in untreated controls. If symbol is below the zero line, then the reverse is true. If error bars do not equal or cross zero line, difference is significant. Letters above symbols indicate significant results for total (a), nonnative (b), and native (c) species. Arrows indicate application of restoration treatments.

2000. The 2000 data were combined with 2001 data for analysis. Fort Valley was subsequently resampled in 2006 and 2011. Mt. Trumbull was subsequently resampled in 2005 and 2010.

2.3. Data analysis

We used the point-line intercept data to estimate aerial cover by summing the number of points per line intercepting a given live plant species and dividing by the total number of possible points. We calculated cover for each species individually and total cover of all points with recorded plants, regardless of species. We used the belt transects to calculate species richness. The number of all (total), nonnative, and native species recorded on the belt transect was summed per plot. The plot totals were then averaged within treatment unit in each block to determine average total, nonnative, and native species richness per treatment per block. In 2003, cheatgrass (*Bromus tectorum*) heavily invaded Mt. Trumbull following a severe drought in 2002 (McGlone et al., 2009a). To determine the influence of cheatgrass on the understory response to treatment we examined all the data from both sites with and without cheatgrass.

Our two study sites were sampled in different years using different field crews. To account for interannual climatic variability and field estimate variability among observers, we have conducted all analyses using standardized data. We tested for trends in total, native, and nonnative aerial cover and species richness for each site using Cohen's *d* (also known as Hedges's *g*) effect size analysis (Hedges, 1981; Cohen, 1988). Effect size analysis was developed to allow for comparison of data from multiple sites (Gurevitch and Hedges, 1999). For each test variable we calculated a *d* statistic using the following equation:

$$d = \frac{m_2 - m_1}{s_{pooled}},$$

where the pooled standard deviation is:

$$s_{pooled} = \sqrt{\frac{(n_2 - 1)s_2^2 + (n_1 - 1)s_1^2}{n_1 + n_2 - 2}},$$

m_1 is the mean of a control unit, m_2 is the mean of a treated unit, $n_1 = 20$ is the sample size for each control unit, $n_2 = 20$ is the sample size for each treated unit, s_1^2 is the variance for a control unit, and s_2^2 is the variance for a treated unit (Hedges, 1981; Cohen, 1988). We calculated a mean *d* statistic for each test variable among the blocks for each study site and determined a 95% confidence interval (CI) for each mean *d* statistic (Nakagawa and Cuthill, 2007). We generated means and measures of variability using JMP software (version 8.0; SAS Institute, Inc., 2008). We calculated the *d* statistics manually.

We also tested for differences in relative nonnative cover and species richness. We calculated relative nonnative cover and richness by dividing the nonnative cover or richness per plot by the total cover or richness per plot, times 100. We used ANOVA to test for differences between sites for the main effects of site, treatment, and year as well as all possible interactions. We also tested for differences within site for the main effects of treatment and year as well as the treatment by year interaction. To test for differences

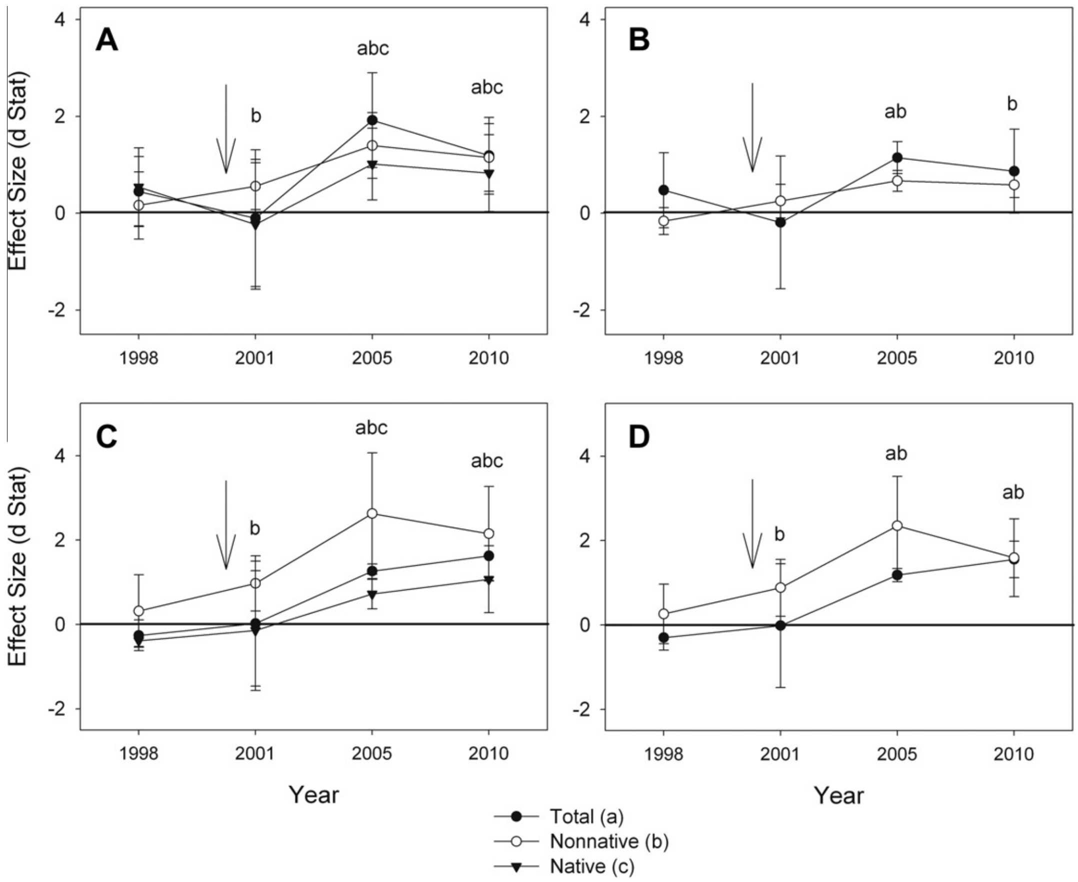

Fig. 2. Effect size results for the Mt. Trumbull study site. Top panels show cover including cheatgrass (A) and excluding cheatgrass (B). Bottom panels show richness including cheatgrass (C) and excluding cheatgrass (D). Error bars show 95% CI. If symbol is above the zero line, magnitude of response was greater in treated units than in untreated controls. If symbol is below the zero line, then the reverse is true. If error bars do not equal or cross zero line, difference is significant. Letters above symbols indicate significant results for total (a), nonnative (b), and native (c) species. Arrows indicate application of restoration treatments.

within significant year or treatment by year interaction results, we used Tukey's HSD post hoc analysis. We tested for the assumptions of normality and homogeneity of the data through visual assessment of histograms. The richness data, both with and without cheatgrass, met the assumptions of normality and homogeneity. The cover data, both with and without cheatgrass, were $\ln(x + 0.5)$ transformed to control for the influence of zeros on normality of distribution. All ANOVA analyses were conducted using JMP software (version 8.0; SAS Institute, Inc., 2008).

3. Results

3.1. Understory trends in response to treatment

Cohen's *d* trend analysis showed both sites, total, nonnative, and native cover and richness had a significantly greater response to treatment as compared to the controls (Figs. 1 and 2). The Fort Valley study site showed a significant positive response for all variables by 2006 that continued to be significant by 2011 (Fig. 1). Native cover had a greater positive response to treatment than nonnative cover. Native and nonnative richness had a similar magnitude of response. Removal of cheatgrass from the analysis had no significant effect on the results for any variable (Fig. 1B and D).

The Mt. Trumbull study site had a more varied response to treatment, but most variables showed a significant positive response to treatment by 2005 that was maintained into 2010 (Fig. 2). Both nonnative cover and richness showed a stronger response to treatment than native cover and richness. The removal of cheatgrass from the analysis reduced the effect size of treatment response for total and nonnative cover as well as total and nonnative richness (Fig. 2B and D). By 2010, the total cover treatment response was no longer significant when cheatgrass was excluded from analysis (Fig. 2B). This implies that the significant positive response of total cover of all species in 2010 was primarily driven by greater cheatgrass cover.

3.2. Relative nonnative contribution to understory

When we compared ANOVA results from the two study sites, relative nonnative cover was significant for site and treatment regardless of whether cheatgrass was included or excluded from the analysis (Table 1). Mt. Trumbull had greater relative nonnative cover than Fort Valley regardless of treatment and the treated units had greater relative nonnative cover than the controls regardless of site (Fig. 3A). These results were consistent whether cheatgrass was included in the analysis or not. Neither year nor any interaction had a significant ANOVA result. Relative nonnative species richness had a significant between site response to treatment regardless of whether cheatgrass was included or excluded from the analysis (Table 1). The treated units had greater relative nonnative species richness regardless of site (Fig. 3B–D). Neither year nor site nor any interaction had a significant ANOVA result.

At Fort Valley, relative nonnative cover was not significant regardless of whether cheatgrass was included in the analysis (Table 1; Fig. 3A). Prior to treatment, Dalmatian toadflax (*Linaria dalmatica*) and common mullein (*Verbascum thapsus*) had an

Table 1
Significant ANOVA results for relative nonnative cover and richness, both including and excluding cheatgrass.

Response variable	*F* statistic	*p* value
Cover all species		
Between sites		
Model	5.13	<0.001
Site	24.03	<0.001
Treatment	21.26	<0.001
Fort Valley		
Model	2.01	0.112
Mt. Trumbull		
Model	3.30	0.013
Treatment	12.38	0.002
Cover excluding cheatgrass		
Model	2.16	0.047
Site	7.92	0.009
Treatment	13.10	0.001
Fort Valley		
Model	2.01	0.112
Mt. Trumbull		
Model	1.78	0.128
Richness all species		
Between sites		
Model	7.55	<0.001
Treatment	44.96	<0.001
Fort Valley		
Model	20.05	<0.001
Year	10.95	<0.001
Treatment	74.74	<0.001
Year by treatment	11.31	<0.001
Mt. Trumbull		
Model	1.78	0.128
Year	3.26	0.042
Treatment	30.98	<0.001
Richness excluding cheatgrass		
Between sites		
Model	5.08	<0.001
Treatment	34.28	<0.001
Fort Valley		
Model	20.91	<0.001
Year	20.51	<0.001
Treatment	77.60	<0.001
Year by treatment	11.69	<0.001
Mt. Trumbull		
Model	1.78	0.128
Treatment	30.98	<0.001

average total cover of <0.01% in the control and treated units. By 2011, Dalmatian toadflax and common mullein were ubiquitous in the treated units at Fort Valley (Table 2). Nonnative speices cover remained low, however, with Dalmatian toadflax having the greatest average cover (0.23% in treated units) of any nonnative species. Relative nonnative richness was significant for treatment and year, as well as the treatment by year interaction, regardless of whether cheatgrass was included in the analysis (Table 1; Fig. 3B and C). In 2011, the treated units had significantly greater relative nonnative richness (8.578%; SE = 0.778) than the control units in any year (e.g. 2011 control relative nonnative richness = 3.198%; SE = 0.778). Prior to treatment, only six nonnative species were detected at Fort Valley and only two, Dalmatian toadflax and common mullein, are listed as noxious in at least one state (Table 2). By 2011, 12 nonnative species were detected and four additional species listed as noxious in at least one state were detected: cheatgrass, musk thistle (*Carduus nutans*), bull thistle (*Cirsium vulgare*), and field bindweed (*Convolvulus arvensis*).

At Mt. Trumbull, relative nonnative cover was significantly greater in the treated units when cheatgrass was included in the analysis, but not when cheatgrass was excluded (Table 1; Fig. 3A). By 2010, cheatgrass had greater average cover in the treated units (5.05%) than any other non-tree species, with bottlebrush squirreltail (*Elymus elymoides*) having the next greatest average cover (2.58%). Surprisingly, considering the large contribution of cheatgrass to the understory cover at Mt. Trumbull, there was no significant site × year × treatment interaction, even when cheatgrass was included in the analysis ($F = 0.12$; $p = 0.88$). This is possibly an artifact of the high variability of the data and low replication. Common mullein was also ubiquitous in the treated units by 2010 (Table 2), but the average cover was low (<0.01%). Relative nonnative richness was significant for treatment and year when cheatgrass was included in the analysis, but was only significant for treatment when cheatgrass was excluded (Table 1; Fig. 3B and D). As with relative nonnative cover, none of the interactions were significant. Prior to treatment, the Mt. Trumbull study sites contained 10 nonnative species of which three (cheatgrass, field bindweed, and common mullein) are listed as noxious weeds in at least one state (Table 2). By 2010, we detected 14 nonnative species including two additional species listed as noxious weeds in at least one state: crossflower (*Chorispora tenella*) and Scotch cottonthistle (*Onopordum acanthium*).

4. Discussion

Restoration in both forests reliably increased understory cover and richness, but the response was highly varied between the two sites. The increased native and nonnative cover and richness were typically detectable after 5 years and the overall trends remained consistent after 10 years. After 10 years, however, Fort Valley was dominated by native species, while Mt. Trumbull was dominated by a single nonnative species: cheatgrass. These results support our first and second hypotheses: (1) native understory will increase in cover and species richness in response to the ecological restoration and (2) nonnatives will also increase in response to treatments. The magnitude of nonnative increase was greater at Mt. Trumbull for both cover and richness than at Fort Valley. Due to the difference in the response of nonnative species to treatments and the lack of a significant increase in total cover at Mt. Trumbull when cheatgrass was removed from the analysis, we reject our third hypothesis that the understory response to ecological restoration will be consistent in both study sites.

Disturbances, such as those associated with fire, tree removal, and/or grazing have often been linked to nonnative encroachment (D'Antonio and Vitousek, 1992; Hobbs and Huenneke, 1992; Brooks et al., 2004). The degree of post-disturbance invasion varies from strong, with nonnatives constituting a substantial component of the understory (e.g. – Wienk et al., 2004; Floyd et al., 2006; Dodge et al., 2008), to mild, with nonnatives only detected in trace amounts (e.g. – Laughlin et al., 2004; Kuenzi et al., 2008; Fornwalt et al., 2010). The intensity of nonnative invasion is often correlated with severity of disturbance (e.g. – Wienk et al., 2004; Dodge et al., 2008), but this relationship is not reliable. For example, Kuenzi et al. (2008) reported low levels of invasion after a wildfire in Arizona, even in severely burned areas. After the Hayman Fire in Colorado, Fornwalt et al. (2010) reported nonnative encroachment increased with increasing fire severity, but nonnative cover and richness remained low. Conversely, given proper climatic conditions substantial invasions have been documented even with only minor disturbances (Evans et al., 2001; Belnap and Phillips, 2001).

Considering the similarities in treatment prescription and implementation, the disparate responses of the two sites to restoration treatments highlights the potential for variability in post-disturbance successional trajectories. Both Fort Valley and Mt. Trumbull had areas of severe disturbance, but the response to treatment was different. At Fort Valley, disturbances associated with mechanical tree harvesting and slash pile burning resulted in increased nonnatives in the understory and seed bank, but the

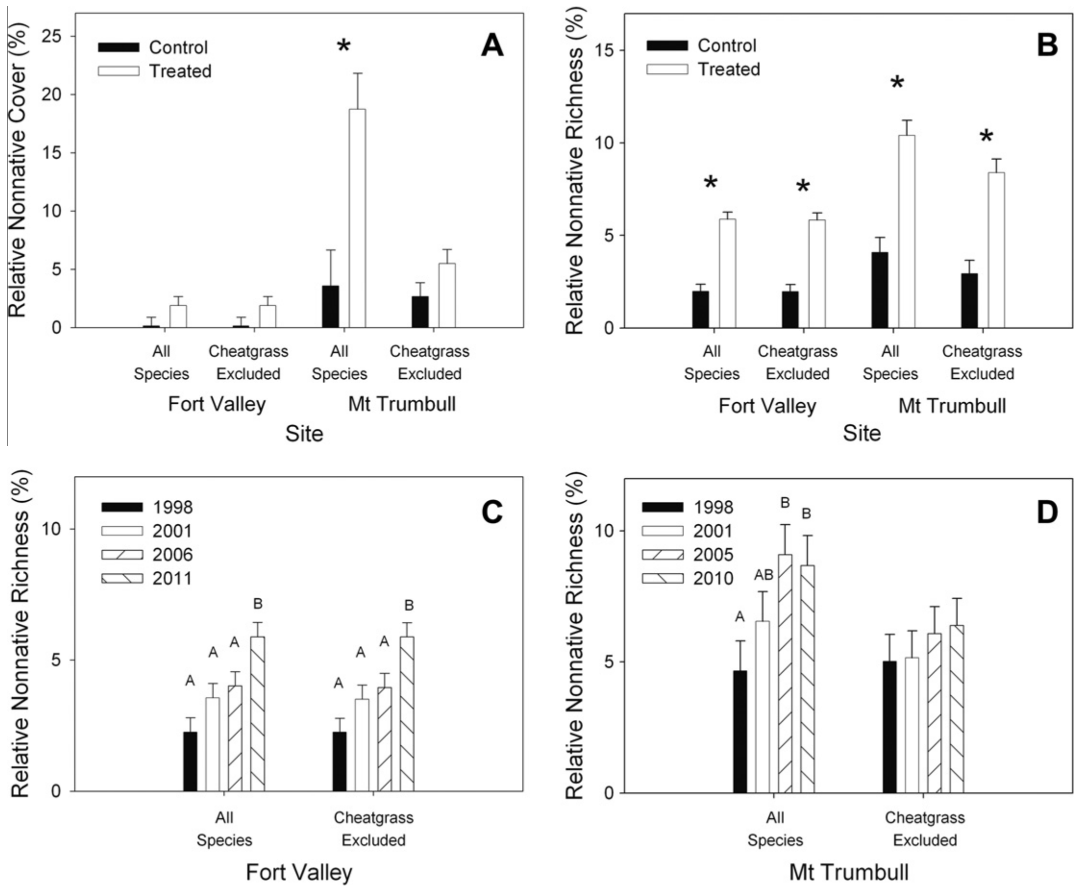

Fig. 3. ANOVA results for relative nonnative cover (A) and relative nonnative species richness (B) for the main effect of treatment within site and relative nonnative richness for the main effect of year at Fort Valley (C) and Mt. Trumbull (D). All graphs show data both including (all species) and excluding cheatgrass. The error bars represent one standard error. Significant differences for the main effect of treatment within site (A and B) are indicated with an asterisk. Significant differences for the main effect of year within site (C and D) and indicted by different letters.

increases were typically isolated to the vicinity of slash piles (Korb et al., 2004). In the first two years after treatment, Mt. Trumbull experienced limited increases in the nonnative component of the understory (Fig. 3; McGlone et al., 2009a,b). By 2010, however, nonnative cover and richness had increased significantly throughout the treated units and often dominated the landscape (Fig. 2).

The fact that Mt. Trumbull was heavily invaded by nonnative while Fort Valley was not is likely the result of conditions at the time of restoration treatment implementation. Prior to treatment, Fort Valley contained a nonnative component to the plant community, including the noxious weed Dalmatian toadflax. Dalmatian toadflax is a species that responds positively to fire and has been perceived as a transformer species (*sensu* Richardson et al., 2000) in other ecosystems (D'Antonio et al., 2004; Dodge et al., 2008). Pretreatment cover of Dalmatian toadflax was low. After treatment, Dalmatian toadflax increased, but remained a minor component of the understory at Fort Valley (Stoddard et al., 2011). Mt. Trumbull, like Fort Valley, contained a nonnative component to the plant community prior to treatment including cheatgrass, a species that responds positively to fire and is considered a transformer species (D'Antonio and Vitousek, 1992; Brooks et al., 2004; D'Antonio et al., 2004). Unlike Dalmatian toadflax at Fort Valley, cheatgrass was prevalant at Mt. Trumbull prior to treatment. While cheatgrass did not expand its population detectably in the first years after treatment, subsequent disturbances associated with a severe drought in 2002 resulted in a greatly increased cheatgrass population at Mt. Trumbull (McGlone et al., 2009a) that has remained stable (McGlone et al., 2011).

Posttreatment differences in plant community development between study sites may also be a function of differences in pretreatment soil seedbanks. Baseline soil seedbank studies from both Fort Valley and Mt. Trumbull prior to ecological restoration treatments indicate that common mullein was the most common species in the study area (Fort Valley: 566; Mt. Trumbull: 940 seeds/m^2; Korb et al., 2005). Fort Valley had slightly higher total species richness in the soil seed bank (Fort Valley: 24 species; Mt. Trumbull: 19 species). The two sites differed substantially, however, in the higher number of native perennial graminoid species detected in the soil seed bank at Fort Valley (6 species) when compared to Mt. Trumbull (1 species), with bottlebrush squirreltail the only native perennial grass species detected in the soil seed bank at Mt. Trumbull. Seed banks at both sites contained potential transformer species. Dalmatian toadflax seeds were present in the soil at Fort Valley prior to treatment, but were not among the most abundant species (Korb et al., 2005). At Mt. Trumbull, however, the soil seed bank in stands dominated by New Mexico locust (*Robinia neomexicana*) and big sagebrush (*Artemisia tridentata*) contained approximately 193 cheatgrass seeds/m^2 (Springer, 1999). Prefire cheatgrass seedbank, as a function of prefire cheatgrass cover, is considered the strongest determinant of postfire cheatgrass dominance in ponderosa pine forests (Keeley and McGinnis, 2007).

While the actual contribution of cattle grazing to the cheatgrass invasion on Mt. Trumbull is unknown, the differences in grazing history between Fort Valley and Mt. Trumbull cannot be ignored. Fort Valley has not been actively grazed by cattle for over a century, while Mt. Trumbull has had active grazing for most of that

Table 2
Frequency of nonnative species encountered at the Mt. Trumbull (n = 80 plots) and Fort Valley (n = 60 plots) study sites, expressed as a percentage of control or treated plots on which each species was found (± one standard error in parentheses). Species in bold are listed as noxious in at least one state (USDA NRCS, 2012).

Species	Common name	Fort Valley				Mt. Trumbull			
		1998		2011		1998		2010	
		Control	Treatment	Control	Treatment	Control	Treatment	Control	Treatment
Bromus inermis	Smooth brome	–	–	–	1.7(1.7)	–	1.3(1.3)	1.3(1.3)	1.3(1.3)
Bromus tectorum	**Cheatgrass**	–	–	**3.3(1.7)**	**8.3(6.0)**	**10.0(3.5)**	**25.0(20.1)**	**23.8(9.9)**	**92.5(6.0)**
Carduus nutans	**Musk thistle**	–	–	–	**3.3(1.7)**	–	–	–	–
Chorispora tenella	**Crossflower**	–	–	–	–	–	–	**1.3(1.3)**	**7.5(4.8)**
Cirsium vulgare	**Bull thistle**	–	–	**1.7(1.7)**	**23.3(7.3)**	–	–	–	–
Convolvulus arvensis	**Field bindweed**	–	–	–	**6.7(6.7)**	–	**1.3(1.3)**	–	**6.3(3.8)**
Lactuca serriola	Prickly lettuce	–	–	11.7(1.7)	40.0(11.5)	–		3.8(2.4)	30.0(15.9)
Leonurus cardiaca	Common motherwort	–	–	–	–	–	5.0(3.5)	–	6.3(4.7)
Linaria dalmatica	**Dalmatian toadflax**	**5.0(2.9)**	**21.7(9.3)**	**16.7(6.0)**	**85.0(10.4)**	–	–	–	–
Marrubium vulgare	Horehound	–	–	–	–	–	–	–	1.3(1.3)
Medicago lupulina	Black medick	–	–	–	1.7(1.7)	–	–	–	–
Medicago sativa	Alfalfa	–	–	–	1.7(1.7)	–	–	–	–
Melilotus officinalis	Yellow sweet clover	1.7(1.7)	–	–	–	–	–	–	–
Onopordum acanthium	**Scotch cottonthistle**	–	–	–	–	–	–	–	**1.3(1.3)**
Polygonum aviculare	Prostrate knotweed	–	1.7(1.7)	–	–	–	–	–	–
Polygonum convolvulus	Black bindweed	–	–	–	–	–	7.5(7.5)	1.3(1.3)	20.0(11.4)
Sisymbrium altissimum	Tall tumblemustard	–	–	–	–	–	–	–	11.3(11.3)
Taraxacum officinale	Common dandelion	10.0(2.9)	6.7(1.7)	15.0(7.6)	36.7(12.0)	2.5(1.4)	–	–	5.0(5.0)
Thinopyrum intermedium	Intermediate wheatgrass	–	–	–	–	–	–	–	1.3(1.3)
Tragopogon dubius	Yellow salsify	1.7(1.7)	3.3(1.7)	3.3(1.7)	30.0(20.8)	1.3(1.3)	8.8(8.8)	3.8(3.8)	35.0(12.4)
Verbascum thapsus	**Common mullein**	**26.7(9.3)**	**16.7(7.3)**	**30.0(12.6)**	**88.3(6.0)**	**17.5(4.3)**	**26.3(11.4)**	**38.8(14.6)**	**85.0(13.4)**

time period. Cattle were reintroduced to Mt. Trumbull after a 3-year exclusion in August 2002, approximately coincident with germination of the cheatgrass plants detected in the 2003 invasion. Cattle grazing may have facilitated the introduction and dispersal cheatgrass seeds thus contributing to the establishment of the cheatgrass seed bank. The winter and spring pastures for the Mt. Trumbull cattle herd are heavily invaded by cheatgrass (Whit Bunting, BLM Rangeland Management Specialist, Personal Communication). Past research has shown that cattle grazing has facilitated the persistence of cheatgrass, particularly in dry years (Sorensen and McGlone, 2010).

Lastly, differences in restoration success may be a function of intrinsic and extrinsic characteristics of the two sites. The likelihood of successful establishment and persistence of nonnative plant species, particularly cheatgrass, is greatly reduced at wetter high elevation sites than at drier, low elevation sites (Pierson and Mack, 1990; Keeley et al., 2003). The Fort Valley site is both higher in elevation and receives greater annual precipitation than Mt. Trumbull. Furthermore, the extent of an ecosystem's historical range is considered a factor in determining the site potential for successful restoration (Palik et al., 2000). The Mt. Trumbull site is an isolated sky island mountain system with ponderosa pine forests occurring at only the highest elevations. Fort Valley is within the largest contiguous ponderosa pine forest in North America.

5. Conclusions

There are numerous parameters to consider when assessing the success of an ecological restoration project. The Society for Ecological Restoration (SER, 2004) defines a restored ecosystem as containing "a characteristic assemblage of the species that occur in the reference ecosystem and that provide appropriate community structure," consisting "of indigenous species to the greatest practicable extent," and being "sufficiently resilient to endure the normal periodic stress events in the local environment that serve to maintain the integrity of the ecosystem." Targets for restoring southwestern ponderosa pine forests frequently include reduction of the potential for sustained crown fires and promotion of a robust native understory community (Fulé et al., 1997; Moore et al., 1999; Laughlin et al., 2006). The Fort Valley study site was successful at achieving both of these goals; tree canopy cover has been reduced (Korb et al., 2007) and native understory cover and richness has been increased. At Mt. Trumbull the risk of sustained crown fire has been reduced (Roccaforte et al., 2010) and the native understory has greater richness than the untreated control units and pretreatment conditions. The Mt. Trumbull restoration project is compromised, however, by the persistent dominance of cheatgrass and the lack of sustained increases in native understory cover. While several nonnative species are capable of invading areas disturbed by fire and/or tree removal, cheatgrass is a recurring threat to higher elevation areas of the Southwest (Keeley et al., 2003; Floyd et al., 2006; Owen et al., 2011; McGlone et al., 2011). Considering the severe ecological impacts of cheatgrass invasions in areas such as the Great Basin, it is difficult to perceive any restoration project that has been invaded by cheatgrass as successful.

Our study demonstrates the potential for highly varied outcomes of ecological restoration projects using a similar approach to establish reference conditions. The success at Fort Valley and lack of success at Mt. Trumbull emphasizes the need for adaptive management by practitioners, particularly in regards to site selection and modification of restoration treatments to include nonnative mitigation. We recommend that managers prioritize areas for restoration treatments that contain a very low nonnative species presence. Managers should particularly avoid areas that contain established populations of transformer species that are known or suspected to be aggressive invaders in the region or in similar ecosystems, (e.g. cheatgrass, star-thistle (*Centaurea* sp.), medusahead (*Taeniatherum caput-medusae*), etc.).

Ecosystems that contain established populations of aggressive nonnatives may be of management priority for restoration and we do not propose that such sites be excluded from restoration management. We do, however, recommend nonnative mitigation activities prior to restoration treatment in order to minimize risk of a vegetation community shift to nonnative dominance. Improvements in herbicide and biocontrol technologies are expanding management options for nonnative mitigation. In general, however, implementation of a single mitigation treatment is insufficient for sustained nonnative species control (e.g. Reever

Morghan and Seastedt, 1999; Owen et al., 2011). Areas of high management priority with high risk of invasion (e.g. wildland–urban interfaces) may require a multi-staged approach to restoration with assessment and nonnative mitigation occurring before, during, and after treatment implementation. Unfortunately, little is known about pretreatment threshold levels of nonnative populations that put an ecosystem at risk of severe invasion. Additionally, advances in herbicide and biocontrol technology may alter pretreatment threshold levels in the future. Our study highlights that few nonnatives are truly aggressive invaders. Of the 24 nonnative species detected on the two sites combined, 13 were present prior to treatment, but only one species, cheatgrass, became a severe invader.

Extensive nonnative mitigation practices are expensive and time consuming. Additionally, management agencies will be unable to implement restoration projects at rates fast enough to negate the risk of catastrophic wildfire in all forests. We therefore recommend that ecological restoration projects be triaged for maximum likelihood of success and not risk compromising the outcome of the project in favor of maximizing the area treated.

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