Ten years of vegetation assembly after a North American mega fire

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Abstract

Altered fuels and climate change are transforming fire regimes in many of Earth's biomes. Postfire reassembly of vegetation – paramount to C storage and biodiversity conservation – frequently remains unpredictable and complicated by rapid global change. Using a unique data set of pre and long-term postfire data, combined with long-term data from nearby unburned areas, we examined 10 years of understory vegetation assembly after the 2002 Hayman Fire. This fire was the largest wildfire in recorded history in Colorado, USA. Resistance (initial postfire deviance from prefire condition) and resilience (return to prefire condition) declined with increasing fire severity. However, via both resistance and resilience, 'legacy' species of the prefire community constituted >75% of total plant cover within 3 years even in severely burned areas. Perseverance of legacy species, coupled with new colonizers, created a persistent increase in community species richness and cover over prefire levels. This was driven by a first-year increase (maintained over time) in forbs with short life spans; a 2–3-year delayed surge in long-lived forbs; and a consistent increase in graminoids through the 10th postfire year. Burning increased exotic plant invasion relative to prefire and unburned areas, but burned communities always were >89% native. This study informs debate in the literature regarding whether these increasingly large fires are 'ecological catastrophes.' Landscape-scale severe burning was catastrophic from a tree overstory perspective, but from an understory perspective, burning promoted rich and productive native understories, despite the entire 10-year postfire period receiving below-average precipitation.

Keywords: disturbance, exotic species, fire severity, Hayman Fire, *Pinus ponderosa*, resilience, resistance, succession, vegetation change

Introduction

Globally, wildfires burned over 300 Mha annually between 1997 and 2011 (Giglio *et al.*, 2013). Fires further affect nonburned land and the atmospheric system in numerous ways, such as by emitting 2.5 Pg C yr^{-1} (Randerson *et al.*, 2012). Fire extent and severity are anticipated to increase in many biomes in coming decades, underscoring importance of understanding fire as an agent of global change (Adams, 2013). Moreover, postfire ecosystem dynamics have feedbacks for other elements of global change, such as exotic species invasions, native biodiversity conservation, C storage, hydrological cycling, and ecological services provided to humans (Stoy *et al.*, 2008; Abella & Engel, 2013; Law *et al.*, 2013).

Vegetation assembly following disturbances such as fire partly depends on ecosystem resistance and resilience and disturbance severity (Bruelheide & Luginbühl, 2009; Fornwalt *et al.*, 2010; Harvey & Holzman, 2014). Resistance is a system's ability to minimize change incurred through disturbance, indicated by high similarity of pre and immediate postdisturbance conditions (Belote *et al.*, 2012). Resilience is ability to return to a predisturbance state, indicated by increasing similarity through time to predisturbance condition (Halpern, 1988). Increasing disturbance severity (e.g., increasing mortality of organisms) can reduce both resistance and resilience, including adaptive ability to climate change (Falk *et al.*, 2011). Although ecosystem resistance and resilience are fundamental to developing land management and conservation policies (e.g., whether active restoration is mandated), several recent reviews have noted key knowledge gaps regarding postdisturbance community assembly in an era of global change (e.g., Abella, 2010; Adams *et al.*, 2012; Anderson-Teixeira *et al.*, 2013). For instance, given climate change and biotic invasions, resilience to predisturbance condition is uncertain (Lin & Petersen, 2013). With disturbances such as wildfire capable of leaving legacies for centuries, improving our

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ability to predict pathways of ecosystem change is anticipated to be critical for preventing species extinctions and conserving ecosystem functions in coming decades (Prober *et al.*, 2007; Knox & Clarke, 2012; Adams, 2013).

After a century under a policy of fire suppression, dry coniferous forests of western North America provide a dramatic example of a biome being transformed by wildfires of unprecedented size and severity (Falk *et al.*, 2011). Annual area burned since 1986 has increased more than sixfold over previous decades (Westerling *et al.*, 2006). The largest fires in recorded history have occurred in the 2000s in several western USA states, such as the 56 000-ha Hayman Fire in 2002 (Colorado), 147 000-ha Milford Flat Fire in 2007 (Utah), 218 000-ha Wallow Fire in 2011 (Arizona), and the 120 000-ha Whitewater-Baldy Complex Fire in 2012 (New Mexico). These, and numerous similarly large fires such as in Australia, have become so large they are termed 'mega fires' (Adams, 2013). Mega fires are already a dominant feature impacting the global landscape and the prognosis is for them to continue (Adams, 2013). Understanding postfire vegetation assembly is a critical step in assessing whether much of western North America will change from a net C sink to source (Hurteau *et al.*, 2011; Law *et al.*, 2013), convert to nonforest cover (Savage & Mast, 2005), accelerate exotic species invasion (Fornwalt *et al.*, 2010), sustain native biodiversity (Keyser *et al.*, 2008), or provide watershed functions (Adams *et al.*, 2012).

Considerable variability has characterized postfire vegetation assembly after wildfires in western coniferous forests, and general principles regarding key components of postfire vegetation change remain elusive. First, the relative proportion of 'legacy' (present before fire) and 'new' (postfire colonizing) species after fire has varied substantially among fires, and temporal persistence of new species is poorly understood (Foxx, 1996; Bataineh *et al.*, 2006; Fornwalt & Kaufmann, 2014). Second, response of native species richness has varied, sometimes declining after fire (e.g., Griffis *et al.*, 2001) and sometimes increasing among burn severities (e.g., Dodge *et al.*, 2008). Third, native plant cover has not displayed consistent changes after fire, and possible relationships with postfire climates are difficult to evaluate because of a paucity of repeated temporal measurements of burned and unburned areas (Lowe *et al.*, 1978; Foxx, 1996; Barclay *et al.*, 2004). Fourth, shrubs, which can form alternative stable states precluding forest re-establishment altogether (Savage & Mast, 2005), have exhibited a full range of decrease, no change, or increase (Pearson *et al.*, 1972; Savage *et al.*, 2013; Fornwalt & Kaufmann, 2014). Fifth, wildfire has generally promoted exotic species invasion, but

magnitude of the invasion has varied and persistence through time is poorly understood (e.g., Dodge *et al.*, 2008; McGlone & Egan, 2009; Fornwalt *et al.*, 2010).

System response to extreme perturbations such as mega fire affords insight difficult or impossible to create experimentally, yet extreme perturbations are challenging to study precisely because their unplanned nature usually precludes information on system state before perturbation. To examine vegetation changes after mega fire, we used a unique set of prefire plant community data and postfire and unburned data repeatedly collected during the first 10 years following fire. We asked: (1) How resistant and resilient is plant community composition after fire and across a fire-severity gradient? We anticipated that resistance and resilience would decline with increasing fire severity and that resilience would increase through time within a burn severity. (2) How did fire affect native species richness and cover through time and across severities? We expected that native richness and cover would initially decline after fire, then increase to equal or exceed prefire levels after severe burning that removed overstory trees as a limitation to understories. (3) What response to fire did shrubs exhibit and was there evidence for type conversion from forest to shrubland? Because large, aggressive shrubs were absent from the local species pool, we did not forecast that shrubs would constitute most of total plant cover. (4) How was exotic species invasion influenced by burn severity and time? We anticipated that exotic species would be most abundant after severe burning but would decline through time after all burn severities. Considerable debate exists regarding whether these large, unprecedented fires are ecological catastrophes (e.g., Haire & McGarigal, 2008; Keane *et al.*, 2008; Swanson *et al.*, 2011). Results provide new insight into ecological response to mega fire increasingly shaping global patterns of ecosystem development. Findings further illustrate conceptual challenges of resilience thinking for biodiversity conservation during global change.

Materials and methods

Study area and plot establishment

Our study area was 60 km southwest of Denver, Colorado, USA, on Pike National Forest lands within and surrounding the Hayman Fire (Fig. 1, Fig. S1). Climate is semiarid, averaging 38 cm yr^{-1} of precipitation, with most falling in spring/early summer from April through June (33% of annual) or in mid- to late summer storms in July–August (37%; Fig. S2; U.S. Forest Service, Manitou Experimental Forest, Woodland Park, CO, USA). January temperature averages -3 °C and July temperature 19 °C. Soils are gravelly and derived from Pike's Peak granite (Moore, 1992). Elevations range from 2000 to

Fig. 1 Repeat panoramas taken from a severely burned ridgetop within the Hayman Fire. Top photo by M.R. Kaufmann, 17 July 2002, approximately 1 month after the area burned. Bottom photo by P.J. Fornwalt, 11 July 2012, 10 years later.

2600 m. Forests are coniferous, dominated by *Pinus ponderosa*, and characteristic of the Colorado Front Range of the Rocky Mountains (Kaufmann *et al.*, 2000). Tree density in 1996/1997, before the Hayman Fire, ranged from ca. 200–1200 trees ha^{-1} and basal area from 11 to 31 m^2 ha^{-1} (Kaufmann *et al.*, 2000). *Pinus ponderosa* comprised >87% of basal area on all slope aspects, except north-facing slopes where basal area of *P. ponderosa* and *Pseudotsuga menziesii* was approximately equal. Before Euro-American settlement in the late 1800s, fire intervals for individual stands near the study area averaged <10 years to >100 years since the year 1197 and are thought to have included mixed surface fire and severe burning at scales of small patches to hectares (Brown *et al.*, 1999; Sherriff & Veblen, 2006). There was subsequently little or no recorded fire after the late 1800s, with human or lightning ignitions quickly suppressed, until the Hayman Fire. Started via human ignition on June 8, 2002, the Hayman fire burned for over a month, consuming 55 750 ha to become the largest wildfire in Colorado's recorded history (Graham, 2003). Fires of the Hayman's extent of severe burning are not generally considered to have occurred in the region during recent millennia (Brown *et al.*, 1999; Kaufmann *et al.*, 2000; Graham, 2003).

Data collection within the Hayman Fire occurred within a 400-ha area in which 20, 1000-m^2 (20 × 50 m) permanent plots were originally established and measured in 1996 or 1997 (Kaufmann *et al.*, 2000; Fornwalt *et al.*, 2003, 2009). Immediately following the fire in 2002, we re-established all plots using their geographic coordinates, prefire overstory stem maps, and remains of plot corner stakes to accurately re-mark plot corners. We classified each plot as burning with high, moderate, or low severity based on the fire's direct effects on the overstory and forest floor. Plots with <50% overstory mortality were categorized as low severity, while moderate-severity plots had ≥50% overstory mortality but only modest levels of crown and forest floor consumption (Fornwalt *et al.*, 2010). High-severity plots were those with 100% overstory tree

mortality and nearly complete forest floor consumption (Fig. 1). Burn severity mapping indicated that ~35% of area within the fire perimeter was burned with high severity, 16% moderate, and 34% low severity, with 15% unburned (Robichaud *et al.*, 2003; Fig. S1). No postfire rehabilitation activities occurred on our plots.

To provide unburned areas for comparison, plots were established within three unburned areas of ~300 ha each. These areas matched environmental conditions, land-use history, and prefire overstory condition of the burn as closely as possible. The unburned areas were just outside the Hayman Fire perimeter, 10–18 km from burned plots. Three plots, each 1000 m^2, were randomly located within each unburned area in 2004. One plot was partially logged in 2011 and was dropped from the data set, leaving 8 unburned plots.

Data collection and data classification

Understory vascular plant composition (excluding tree species) and cover were recorded in modified-Whittaker sampling plots (Stohlgren *et al.*, 1995). Burned plots were surveyed seven times, in 1996 or 1997 (5 or 6 years prefire), annually from 2003 to 2007 (1–5 years postfire), and in 2012 (10 years postfire). Unburned plots were surveyed four times (2004, 2005, 2006, and 2012). Areal cover of each species within each plot was visually categorized to the nearest percent in 10, 1-m^2 subplots. Species presence was noted in two 10-m^2 subplots, one 100-m^2 subplot, and the 1000-m^2 plot. Most plants were recorded to species, but some were only identifiable to genus and we counted them as one species (e.g., *Carex* or *Chenopodium* spp.). Nomenclature follows NRCS [Natural Resources Conservation Service] (2013).

To aid in analysis, species were classified in three ways. First, species in burned plots were classified as either 'legacy' (present aboveground in plots during the prefire survey) or 'new' species (absent in the prefire survey). A species could be

a legacy species in one plot but a new species in another, depending on whether the species was recorded before fire, and was based on presence aboveground rather than potentially only in the soil seed bank. Second, species were classified into one of four groups reflecting life history and growth form: short-lived forbs (annuals, biennials, or annual-perennial life spans), long-lived forbs (perennials), graminoids, and shrubs. Short- and long-lived graminoids were not separated into their own groups because short-lived graminoids were scarce. This classification followed NRCS (2013) and botanical keys (Harrington, 1964; Weber & Wittmann, 2001). Third, species were classified as either native or exotic to the continental USA (NRCS [Natural Resources Conservation Service] 2013).

Data analysis

We analyzed the data set using both multivariate and univariate techniques. For multivariate analyses, we used PC-ORD 6.0 (McCune & Mefford, 1999) to calculate plot-level Sørensen similarity between pre and postfire years using matrices of relative cover (cover species $_i$/$\sum$ all species on a plot). We also used PC-ORD to ordinate community composition (relative cover) of burned plots using nonmetric multidimensional scaling (Sørensen distance, 'slow and thorough' setting). From these ordinations, we further calculated successional vectors, depicting community compositional change between pre and postfire years (McCune & Mefford, 1999). As a measure of the amount of change, we calculated lengths of vectors from vectors standardized to the origin as Euclidean distance between ordination scores of pre and postfire years on each plot.

We examined univariate changes in community similarity (Sørensen index to the prefire community), richness (species 1000 m^{-2}), and cover with respect to burn severity, year, and burn severity $\times$ year using repeated measures analysis of variance in SAS 9.4 (GLIMMIX procedure; SAS Institute Inc., Cary, NC, USA). Richness and cover were examined in total and by three species groups: (1) legacy and new species; (2) short-lived forb, long-lived forb, graminoid, and shrub; and (3) native and exotic. Cover was summed across species for species groups and was square-root transformed to improve distribution and homogeneity of residuals. Models used the spatial power covariance matrix, accommodating correlation between repeated measurements. When a burn severity $\times$ year interaction had a P-value <0.10, we used the 'SLICE' function in SAS to isolate multiple comparisons (Tukey–Kramer adjusted, with significance set at $P < 0.05$) among years within a burn-severity class. When only a main effect of year was significant ($P < 0.05$), we evaluated multiple comparisons (Tukey–Kramer adjusted, $P < 0.05$) by slicing the data into burned (low, moderate, and high severity) and unburned groups.

Results

Study climate and plant community

Precipitation was near or above average for the 1996/1997 prefire sampling years and sharply below average in the fire year of 2002 (Fig. S2). Moreover, all 13 years, encompassing 3 years before and during the fire and 10 postfire years, received less than the long-term average precipitation. Unburned species richness for all four available sample years (2004–2006 and 2012) was quite constant relative to the maximum recorded richness value, whereas burned richness increased during this period. Unburned cover was relatively constant in 2004–2005 and declined in 2006, whereas burned cover increased those years and was also higher than unburned cover 10 years postfire in 2012. These data indicate that in the same climatic period, temporal fluctuations in plant communities differed between burned and unburned plots.

We recorded 281 species, of which 264 (94%) were native and 17 (6%) were exotic, across all plots and years. There were 68 short-lived forb (24%), 136 long-lived forb (48%), 49 graminoid (18%), and 28 shrub species (10%). In 2012 (10 years postfire), species with greatest average cover in descending order (2.8–0.8%) on burned plots included: *Arctostaphylos uva-ursi*, *Carex* spp., *Heterotheca villosa*, *Muhlenbergia montana*, *Yucca glauca*, *Bouteloua gracilis*, *Poa fendleriana*, and *Artemisia frigida*.

Vegetation community dynamics

First-year, postfire community composition was twice as similar to prefire composition in low- and moderate-severity plots than it was in high-severity plots (Fig. 2; Table 1). Moreover, resemblance of the low-severity burned community to the prefire community increased during the 10-year postfire period. More severe burning resulted in either inconsistent changes through time and little net change (moderate severity) or little change through time (high severity) of the burned community relative to the prefire community. Thus, severe burning resulted in both reduced resistance and resilience compared to low-severity burning.

Ordinations illustrated structuring of postfire community assembly by burn severity. There was little to no grouping of plots before fire, but differentiation by burn-severity class increased through time after fire (Fig. 3). By 5 years after fire, plots assembled into a compositional gradient from low, moderate, to high severity, a pattern maintained at 10 years postfire. Moreover, the number of species correlated with community gradients increased through time, with species such as the long-lived forb *Heterotheca villosa* correlated with severe burning. At 10 years postfire, low-severity plots exhibited less deviance (indicated by short successional vectors and low Euclidean distance) from the prefire community than they did at 1
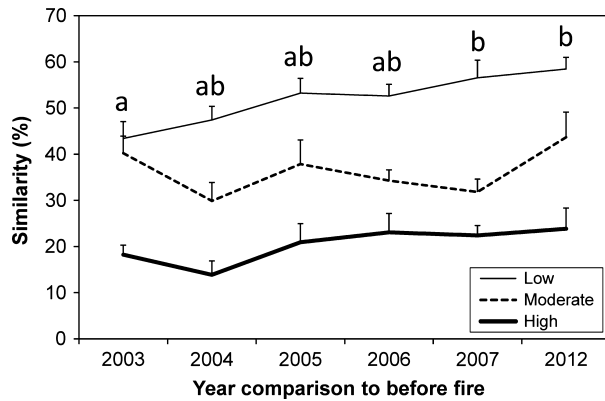
Fig. 2 Mean Sørensen similarity of postfire plant community composition to prefire (1996/1997) composition across burn severities following the Hayman Fire, Colorado, USA. Error bars are standard errors of means. Letters compare means within the low-severity burn class. Only the low-severity burn class exhibited significant differences ($P < 0.05$) in similarity (to prefire condition) through time among postfire years. Community composition at 5 (2007) and 10 years (2012) after low-severity fire was significantly more similar to prefire composition than in the initial postfire year (2003). Plots burned with moderate or high severity showed no significant trend to return to prefire community composition through time.

or 5 years postfire, indicating return to prefire condition (Fig. S3). Meanwhile, deviance of high-severity plots continued to increase, suggesting further divergence from prefire condition.

Species persistence and colonization

Percentages of species from the prefire community (legacy species) persisting in the initial year after fire ranged from 62% in high-severity plots to 81% and 83% in low- and moderate-severity plots (Fig. 4). As of 10 years postfire across burn severities, there were 18 species present before, but not after burning, although none of these species had occupied more than 3 plots before burning. Legacy species richness was quite constant through time and did not differ significantly among any postfire years within any burn severity. Richness of new colonizers was initially similar (13–15 species 1000 m^{-2}) in the first postfire year among severities and was subsequently sustained or increased in one or more postfire years. However, the increase was most consistent in high- and moderate-severity plots, which accrued an average of 27 new species 1000 m^{-2} by 10 years postfire. As of 10 years postfire, there were 8 new species that had colonized at least 5 burned plots, and 6 of these species colonized during the first postfire year and perpetuated 10 years postfire. New

Table 1 Summary of univariate statistical results for 10 years of vegetation dynamics after the Hayman Fire, Colorado, USA.

Understory measure	Year (P-value)	Burn severity (P-value)	Year × burn severity (P-value)
Similarity to prefire (%)			
Sørensen index	**0.005**	**<0.001**	0.087
Total richness (1000 m^2)	**<0.001**	**<0.001**	**<0.001**
Legacy/new richness (1000 m^2)			
Legacy species	0.168	**0.017**	0.444
New species	**<0.001**	**0.005**	**0.003**
Lifeform richness (1000 m^2)			
Short-lived forbs	**<0.001**	**<0.001**	**<0.001**
Long-lived forbs	**<0.001**	**<0.001**	0.151
Graminoids	**<0.001**	0.149	0.148
Shrubs	0.188	0.527	0.624
Native/exotic richness (1000 m^2)			
Native species	**<0.001**	**<0.001**	**0.007**
Exotic species	**<0.001**	**<0.001**	**<0.001**
Total cover (%)	**<0.001**	**0.007**	**0.006**
Legacy/new cover (%)			
Legacy species	**<0.001**	0.657	0.051
New species	**<0.001**	**<0.001**	**<0.001**
Lifeform cover (%)			
Short-lived forbs	**<0.001**	**<0.001**	**<0.001**
Long-lived forbs	**<0.001**	**0.004**	**0.049**
Graminoids	**<0.001**	0.962	**0.011**
Shrubs	**<0.001**	0.539	0.595
Native/exotic cover (%)			
Native species	**<0.001**	**0.032**	**0.024**
Exotic species	**<0.001**	**<0.001**	**<0.001**

P-values in bold are <0.05.

species that colonized the most plots at 10 years postfire included the long-lived forb *Symphyotrichum porteri* (8 new plots); short-lived forbs *Lactuca serriola* (an exotic species; 7 plots), *Epilobium brachycarpum* (7 plots), and *Conyza canadensis* (7 plots); and the long-lived forb *Chamerion angustifolium* (6 plots).

Cover of legacy and new species showed a different pattern than richness (Fig. 4; Table 1). Cover of legacy species was sharply reduced and then consistently increased to even exceed prefire levels by 4–5 years postfire. New colonizers contributed substantial cover after high- and moderate-severity burning, although the proportion of total cover they composed decreased over time owing to a more dramatic increase in cover of legacy species. New colonizers comprised only low cover (~1%) and only a small proportion (~0.05) of total plant cover after low-severity burning, and this contribution did not change significantly through time.
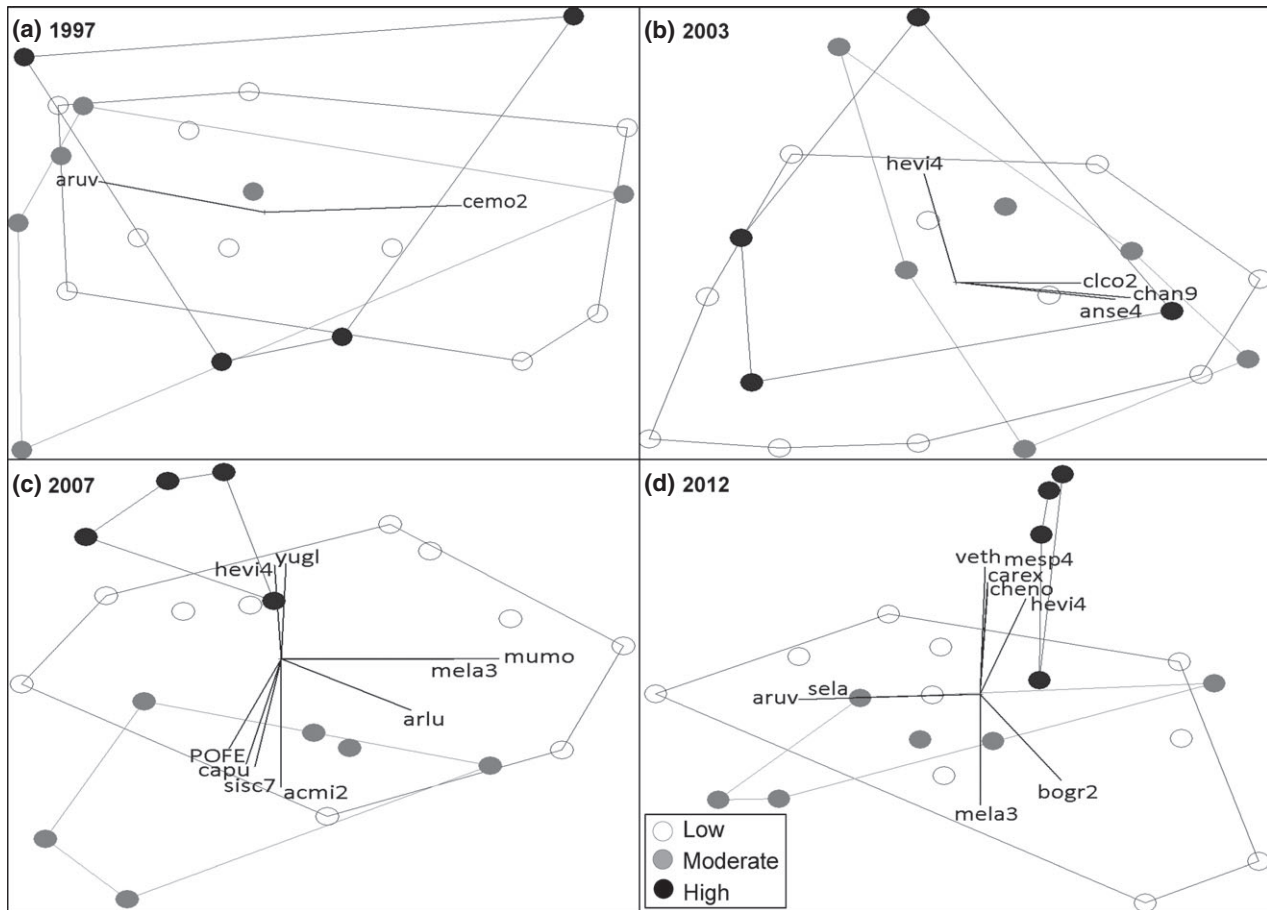
Fig. 3 Nonmetric multidimensional scaling ordination of the (a) prefire 1996/1997 plant community, (b) 1-year postfire, (c) 5-year post-fire, and (d) 10-year postfire community following the 2002 Hayman Fire, Colorado, USA. Plots, grouped by burn severity connected via convex hulls, exhibit differentiation through time, especially for the high-severity class. Vectors display species correlated ($r^2 \geq 0.40$) with plant community gradients. Species abbreviations follow NRCS (2013) codes: acmi2 = *Achillea millefolium*, anse4 = *Androsace septentrionalis*, arlu = *Artemisia ludoviciana*, aruv = *Arctostaphylos uva-ursi*, bogr2 = *Bouteloua gracilis*, capu = *Calamagrostis purpurascens*, carex = *Carex* spp., cemo2 = *Cercocarpus montanus*, chan9 = *Chamerion angustifolium*, cheno = *Chenopodium* spp., clco2 = *Clematis columbiana*, hevi4 = *Heterotheca villosa*, mela3 = *Mertensia lanceolata*, mesp4 = *Mentzelia speciosa*, mumo = *Muhlenbergia montana*, POFE = *Poa fendleriana*, sela = *Sedum lanceolatum*, sisc7 = *Silene scouleri*, yugl = *Yucca glauca*, veth = *Verbascum thapsus*.

Postfire community assembly resulted from persistence of at least half of the prefire species on each plot combined with colonization by new species the first three postfire years and that subsequently remained in the burned community. Legacy species contributed more to plant cover than did new colonizers, but like for richness, the cover contribution of new species remained part of the burned community for all 10 years.

Responses of species by life form and nativity

Postfire community changes manifested from different temporal responses by different groups of species. Postfire total species richness increased by 36%, from 39 ± 1 species 1000 m^{-2} ($\pm$ SEM, $n = 20$) in the prefire community, to 53 ± 2 species in the 10-year postfire community. This increase resulted from a surge in short-lived forbs, less dramatic but still significant increase (by postfire year 3) in long-lived forbs, and maintenance or slight increase in graminoid and shrub richness (Fig. 5). Postfire total plant cover displayed more interannual variation than richness, but increases in the 10-year postfire community were evident and also resulted from overall increases in short-lived forbs (especially in high- and moderate-severity plots) and in long-lived forbs (after depressed cover the first postfire year relative to prefire; Fig. 6). Cover of both graminoid and shrub
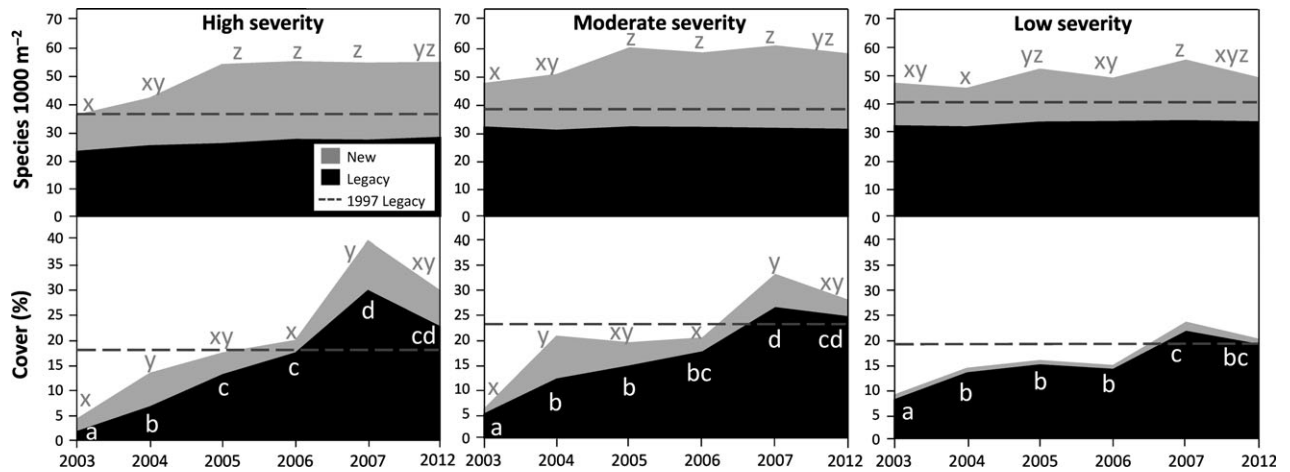
Fig. 4 Dynamics of legacy species present in the prefire (1996/1997) community and influx of new species among burn severities following the 2002 Hayman Fire, Colorado, USA. Letters compare means ($P < 0.05$) separately for legacy species (a, b, c, d) and new species (x, y, z) among years within a burn severity class. Broken lines signify 1996/1997 levels of legacy species in the prefire community.

groups rebounded through time following major reductions from prefire levels. It is further noteworthy that neither richness nor cover exhibited any significant interannual variation on unburned areas in their four available years for any lifeform group, whereas numerous significant differences among these years occurred on burned plots (Figs 5 and 6). Moreover, cover of short-lived forbs, so dramatically increased on burned areas, was negligible (<0.1%) on unburned plots.

Native species dominated richness and cover before and after burning, and their temporal fluctuations often mirrored those of exotic species (Fig. 7; Table 1). Exotic species richness was significantly greater than prefire by 2–3 years after high- and moderate-severity burning. On unburned plots, in contrast, exotic plants were sparse or absent and showed no increase through time. Despite increased exotic plants after burning, exotics still were not a dominant part of the postfire community by 10 years after fire. Their distributions were, however, more extensive after fire. This progression was driven both by new colonizers, where 10 (59%) of the 17 total exotic species recorded during the study were absent from the prefire community, and by expansion of 5 of the 7 species already in the prefire community (Table 2). For example, *Lactuca serriola* was absent before fire but occupied 55% of first-year postfire plots and up to 85% of plots by the 5th postfire year. *Bromus inermis*, *Linaria vulgaris*, *Taraxacum officinale*, *Tragopogon dubius*, and *Verbascum thapsus* all were present in the prefire community, and they invaded 2- to 12-fold more plots after fire.

Discussion

This unique data set enabled evaluating temporal questions regarding community dynamics following mega fire, and there was variable support for our *a priori* expectations. Community resistance and resilience depended on burn severity and the community characteristic considered. Species composition after low and moderate–severity burning showed appreciable resistance to change from prefire condition. Subsequently, areas burned with low severity had greater resilience through convergence toward prefire condition over time, whereas convergence was inconsistent or minimal after moderate and severe burning. Displaying a different temporal trend, species richness was neither resistant to change nor resilient toward prefire condition, owing to an influx of new colonizers that now appear long-term (>10 years) occupants of the burned communities. From a biodiversity perspective, most of these new colonizers were native species and thus burning resulted in communities more native species-rich than before burning. Plant cover was sharply reduced the first postfire year, implying low resistance, then increased to exceed prefire levels at 5 years postfire. The initial low resistance of plant cover might relate both to fire effects and extremely dry conditions in 2002 reducing plant production. It is noteworthy, however, that plant cover consistently increased in all postfire years (except for at 10 years, which still exceeded prefire levels) despite all 10 years receiving below-average precipitation. Postfire dynamics of exotic species mirrored
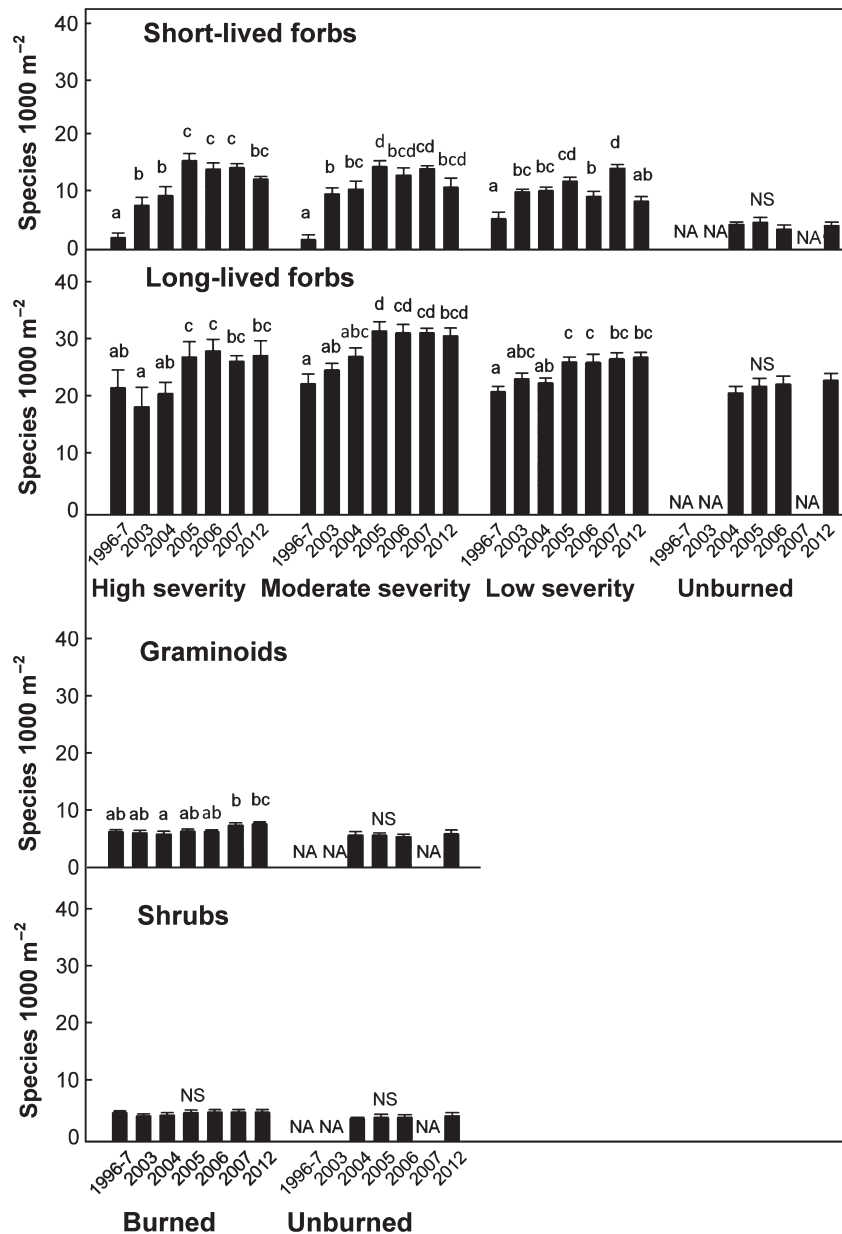
Fig. 5 Species richness of plant groups following the 2002 Hayman Fire, Colorado, USA. Bars are means and error bars are standard errors of means. Groups are displayed by burn severity class for severity × year interactions. Letters separate means through time within a burn severity class (NS = not significant at $P < 0.05$). NA for unburned plots notes data not available.

those of native species, but started from a different prefire baseline. Exotic species were sparse before fire and increased on burned areas, while remaining sparse on unburned areas during the same time period.

Widespread postfire dynamics in western dry forests

Combined with other literature, our results provide insight into broad patterns of understory vegetation

assembly following disturbance in conifer forests of western North America. Previous studies have suggested strong persistence of understory species through disturbance and contingency of postdisturbance vegetation on the predisturbance community (Halpern, 1988; Anderson & Romme, 1991; Turner *et al.*, 1997; Doyle *et al.*, 1998). Our data support these findings: of 147 total species we recorded in the 10-year postfire community, 79% had been part of the prefire community. Previous studies in dry conifer forest have
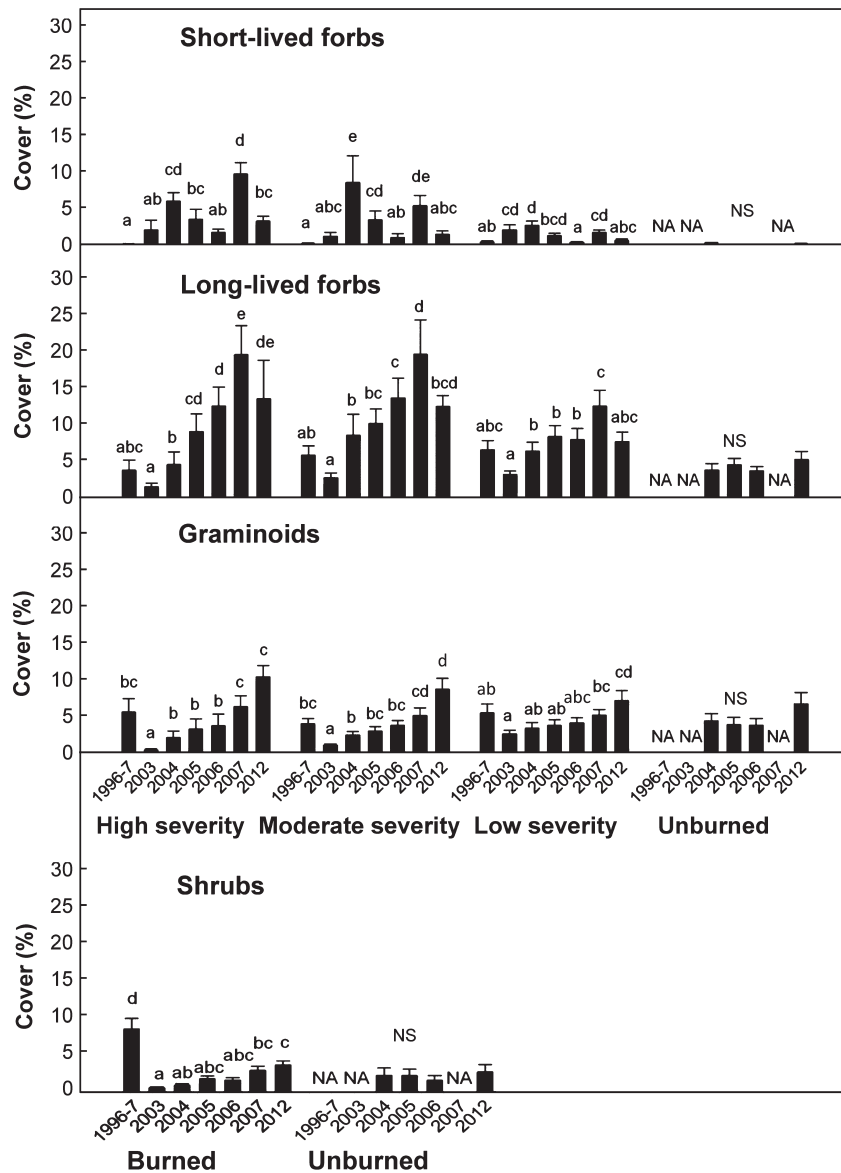
Fig. 6 Cover of plant groups following the 2002 Hayman Fire, Colorado, USA. Bars are means and error bars are standard errors of means. Plant groups are displayed by burn severity class for significant burn severity × year interactions. Letters separate means through time within a burn severity class (NS = not significant at $P < 0.05$). NA for unburned plots notes data not available.

reported variable responses of species richness among wildfire burn severities and between burned and unburned areas. Richness has been both higher (Foxx, 1996; Crawford *et al.*, 2001), and lower in burned than in unburned areas (Griffis *et al.*, 2001; Dodge *et al.*, 2008). We found that richness was higher after fire and higher on burned than unburned areas. Among burn severity classes, richness has not differed among classes (Crawford *et al.*, 2001), been least with severe burning (Dodge *et al.*, 2008), and conversely, been highest with severe burning (Kuenzi *et al.*, 2008; Shive *et al.*, 2013). We found slightly higher richness (~10% greater) after moderate burning, but no appreciable difference in temporal postfire patterns among severities. Variation among studies could stem from numerous reasons, such as differences in fire severity within classes, sampling methods, and prefire condition of study areas (unknown for most studies).

Exotic plants have increased with wildfire (relative to unburned areas) in western dry forests (Merrill *et al.*, 1980; Crawford *et al.*, 2001; Griffis *et al.*, 2001; Barclay *et al.*, 2004; Freeman *et al.*, 2007; Dodge *et al.*, 2008) and been most abundant in severely burned areas (Crawford *et al.*, 2001; Barclay *et al.*, 2004; Freeman *et al.*, 2007; Dodge *et al.*, 2008; Kuenzi *et al.*, 2008; Fornwalt *et al.*, 2010; Shive *et al.*, 2013). Our results
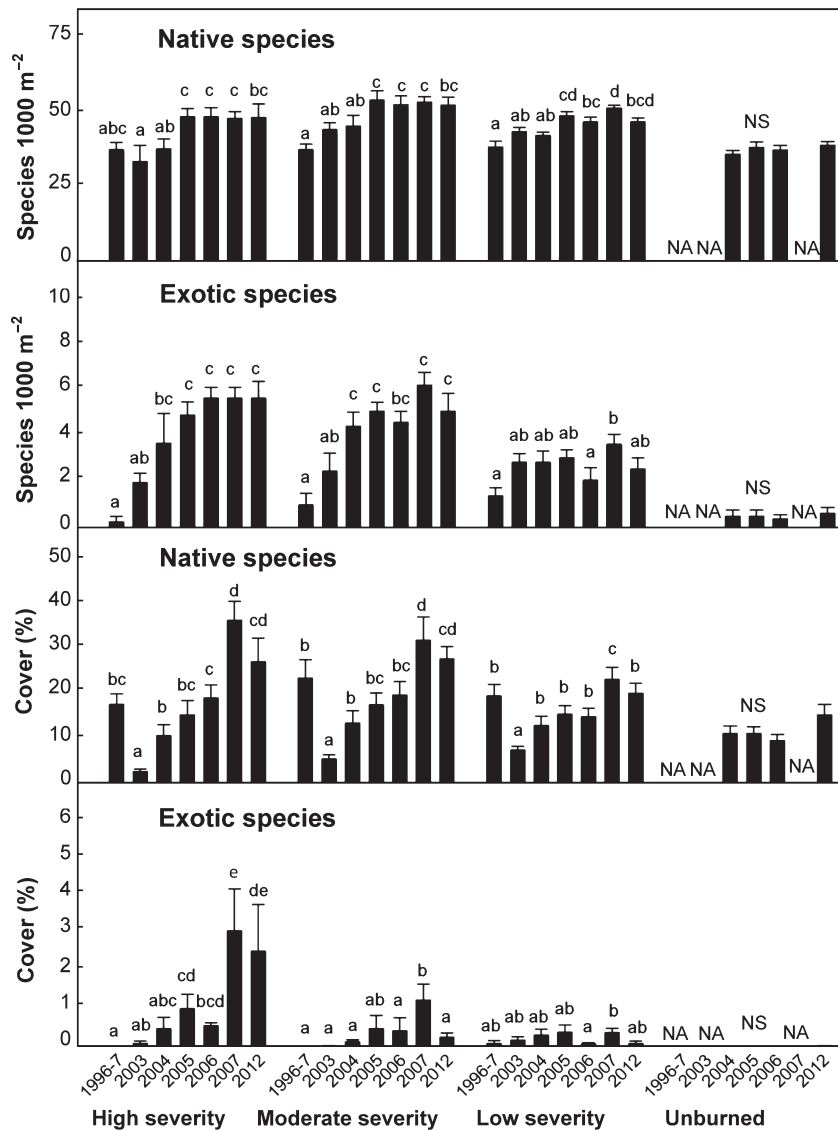
Fig. 7 Species richness and cover of native and exotic species following the 2002 Hayman Fire, Colorado, USA. Bars are means and error bars are standard errors of means. Letters separate means through time within a burn severity class (NS = not significant at $P < 0.05$). NA for unburned plots notes data not available.

reinforce these findings and further showed that exotic plants increased through time after burning. However, relative amounts of exotic plants have sharply differed among studies, and our study reported relatively low amounts of exotic plants, akin to fires examined by Freeman *et al.* (2007) and the Rodeo-Chediski Fire in Arizona (Kuenzi *et al.*, 2008; Shive *et al.*, 2013). Exotics were more dominant after wildfires in northern Arizona (Crawford *et al.*, 2001; Griffis *et al.*, 2001; Dodge *et al.*, 2008), the Dome (Barclay *et al.*, 2004) and Cerro Grand Fires in northern New Mexico (Freeman *et al.*, 2007), and the High Meadow Fire in Colorado (Freeman *et al.*, 2007). Reasons for these differences among studies are unclear and should not relate to differences

in postfire rehabilitation treatments (e.g., seeding) because we considered only untreated areas in these comparisons. Numerous factors could relate to postfire invasion, including presence of exotic plants before fire, proximity to seed sources, condition of the postfire native plant community, and climate during the postfire period (Fornwalt *et al.*, 2010).

Postfire shrub dynamics are also of interest because of potential for type conversion from forest to shrubland, and some previous studies have reported that shrubs were sparse after some fires (Foxx, 1996; Savage & Mast, 2005), while others reported shrub dominance (Savage & Mast, 2005; Shive *et al.*, 2013). We found no evidence for type conversion into shrubland, because

Table 2 Frequency distribution of exotic plant species through time following the Hayman Fire, Colorado, USA.

Species	Percent of plots ($n = 20$)						
	Prefire	Postfire year 1	Postfire year 2	Postfire year 3	Postfire year 4	Postfire year 5	Postfire year 10
Short-lived forbs							
Axyris amaranthoides	0	5	0	0	0	0	0
*Carduus nutans**	0	0	10	15	25	25	20
Lactuca serriola	0	55	55	75	60	85	35
Matricaria discoidea	0	0	0	0	5	0	0
Sonchus asper	0	0	5	0	0	0	0
Tragopogon dubius	5	0	35	45	50	80	60
*Verbascum thapsus**	30	80	90	100	85	100	95
Long-lived forbs							
*Cirsium arvense**	0	25	25	35	25	45	35
*Linaria vulgaris**	5	5	40	20	15	15	35
Taraxacum officinale	40	25	45	60	80	85	70
Graminoids							
Agropyron cristatum	0	0	10	0	0	0	0
Bromus inermis	5	5	5	10	5	20	25
*Bromus tectorum**	0	0	0	0	0	20	20
Phleum pratense	0	0	5	0	5	5	0
Poa annua	5	0	0	0	0	0	0
Poa pratensis	15	5	5	0	0	5	5
Triticosecale rimpaui	0	55	25	50	5	5	0

*Signifies species classified as noxious weed by the State of Colorado.

despite increasing through time after fire, shrubs had still attained less than half of their prefire cover by 10 years postfire. Differences among fires might primarily relate to whether large-statured, aggressive shrub species are in the species pool (not the case at our study sites).

Potential influences of study designs on conclusions

This study's unique inclusion of prefire and unburned data and long-term, repeated postfire measurements likely facilitated inference in several ways. First, our evaluation of questions of resistance and resilience to prefire condition is rarely possible for unplanned events such as wildfires. While our prefire data represent only a single point in time, 1996/1997 likely provided a stringent benchmark when comparing postfire recovery, because the prefire period was wetter than all 10 postfire years (Fig. S2). Prefire data also avoided a need to assume that unburned areas were otherwise similar to burned areas. Precisely because of the enormous size of mega fires, the nearest unburned areas are often tens of kilometers away and may represent different site conditions than those that burned. We were able to locate relatively comparable unburned areas near the fire perimeter, and through repeated measurements, demonstrate that unburned areas exhibited little

temporal change compared to burned areas. Second, prefire and repeated measurements allowed calculation of persistence and colonization of species through time. This provided new insight that almost all species of the overall flora do persist in these ecosystems – even through severe burning – and that newly colonizing species entering the burned community largely become persistent members for at least 10 years. Our analysis revealed little indication that these new species begin declining within a few years after disturbance, as has been reported in some other ecosystems (e.g., Harvey & Holzman, 2014). Third, repeated postfire measurements were crucial for detecting that exotic plants actually increased as the burned community matured.

Implications for forest conservation and resilience framework for global change

Numerous authors have asked whether mega fires are ecological 'catastrophes' (e.g., Haire & McGarigal, 2008; Keane *et al.*, 2008), with some authors suggesting de-emphasizing negative aspects of severe burning (Haire & McGarigal, 2008). Results from the Hayman Fire suggest that severe burning was, in fact, catastrophic from a perspective of overstory trees and maintaining a forest (P.J. Fornwalt, unpublished data). Western conifer tree species do not generally form

persistent soil seed banks and have relatively short seed dispersal distances of ~150 m, poorly equipping them to colonize large, severely burned patches tens of kilometers from the nearest seed sources (Haire & McGarigal, 2010). Recruitment also is contingent upon infrequent combinations of multi-year temperature and precipitation conditions conducive to tree establishment (Savage *et al.*, 2013). Regardless, even if recruitment started now, several centuries are required to grow the several-centuries-old trees killed by severe burning (Kaufmann *et al.*, 2000). Further, patches of severe fire are in fact considered part of the historical Front Range landscape, but the size of severely burned areas in the Hayman Fire is considered unprecedented in the recent evolutionary history of these forests (Brown *et al.*, 1999; Graham, 2003; Sherriff & Veblen, 2006). Thus, from a perspective of conserving forest, outcomes of mega fires in these forests support use of mechanical tree thinning and prescribed fire to reduce fuels and ameliorate fire severity (or reduce size of severe fire) when wildfire inevitably occurs (Fulé *et al.*, 2012). Areas of low and moderate-severity burning support this, as these areas exhibited some tree survival, stimulation of native understories, and tempered exotic plant invasion compared to high-severity burning. Effective fuel treatments have a demonstrated ability to reduce fire severity to attain low and moderate burning likely mimicking many historical fires (Fulé *et al.*, 2012).

Our results also qualify those of Haire & McGarigal (2008) from an understory perspective, as our examination of both herbaceous and shrub species, rather than only woody plants as in Haire & McGarigal (2008), provided further insight into species dynamics. We found that the fire overall stimulated the native understory, while 18 species (16%), all herbaceous, of the prefire community were not recorded on any burned plot at 10 years postfire. Precisely because these 18 species were rare before the fire (none occupied >3 plots), they warrant further attention. Local extinctions of uncommon species could indeed be catastrophic to their regional population persistence. We suggest that evaluations of these types of possibly fire-sensitive organisms are warranted for balanced conclusions regarding beneficial and catastrophic outcomes of continued mega-fire regimes.

Maintaining ecological resilience has emerged as a strategy for conserving biodiversity and ecosystem services during global change (Rist & Moen, 2013). Yet, a major stumbling block has been reconciling numerous definitions and interpretations of resilience, how to measure it, and what ecological features are required to manage for it (e.g., Brand & Jax, 2007; Folke *et al.*, 2010). The underlying assumption is that resilience is desirable. Our results help inform resilience thinking by illustrating importance of considering baseline condition for which resilience is to be defined, time and spatial scales, and vastly different resilience among components within an ecosystem (e.g., tree versus understory layers). Ironically, resilience could be considered undesirable in the context of the prefire baseline, because resilience of prefire condition entails returning to an understory-depauperate, densely treed forest that many ecologists consider degraded (e.g., Keyser *et al.*, 2008; Falk *et al.*, 2011; Savage *et al.*, 2013). Another issue is that from one perspective, the understory community was 'not resilient', because species richness and cover did not return to prefire condition – they dramatically exceeded it. A much longer temporal baseline may be useful for characterizing resilience, such as ranges of forest characteristics prior to anthropogenic fire-regime disruption in the late 1800s. These more open past forests are thought to have been resilient to fire and climatic variation in recent millennia and perpetuated as forest (Brown *et al.*, 1999; Sherriff & Veblen, 2006; Abella *et al.*, 2013). Results suggest that resilience from extreme perturbation is not always desirable, contingent upon preperturbation baseline, and that extreme perturbations can devastate some ecosystem components but benefit other components. Restoration tree thinning or prescribed burning to reduce size of severe fire may optimize conservation of tree canopy cover and stimulation of understory vegetation when wildfire inevitably occurs.

References

Abella SR (2010) Disturbance and plant succession in the Mojave and Sonoran Deserts of the American Southwest. *International Journal of Environmental Research and Public Health*, **7**, 1248–1284.

Abella SR, Engel EC (2013) Influences of wildfires on organic carbon, total nitrogen, and other properties of desert soils. *Soil Science Society of America Journal*, **77**, 1806–1817.

Abella SR, Denton CW, Brewer DG, Steinke RW (2013) Soil development in vegetation patches of *Pinus ponderosa* forests: interface with restoration thinning and carbon storage. *Forest Ecology and Management*, **310**, 632–642.

Adams MA (2013) Mega-fires, tipping points and ecosystem services: managing forests and woodlands in an uncertain future. *Forest Ecology and Management*, **294**, 250–261.

Adams HD, Luce CH, Breshears DD *et al.* (2012) Ecohydrological consequences of drought- and infestation-triggered tree die-off: insights and hypotheses. *Ecohydrology*, **5**, 145–159.

Anderson JE, Romme WH (1991) Initial floristics in lodgepole pine (*Pinus contorta*) forests following the 1988 Yellowstone Fires. *International Journal of Wildland Fire*, **1**, 119–124.

Anderson-Teixeira KJ, Miller AD, Mohan JE, Hudiburg TW, Duval BD, DeLucia EH (2013) Altered dynamics of forest recovery under a changing climate. *Global Change Biology*, **19**, 2001–2021.

Barclay AD, Betancourt JL, Allen CD (2004) Effects of seeding ryegrass (*Lolium multiflorum*) on vegetation recovery following fire in a ponderosa pine (*Pinus ponderosa*) forest. *International Journal of Wildland Fire*, **13**, 183–194.

Bataineh AL, Oswald BP, Bataineh MM, Williams HM, Coble DW (2006) Changes in understory vegetation of a ponderosa pine forest in northern Arizona 30 years after a wildfire. *Forest Ecology and Management*, **235**, 283–294.

Belote RT, Jones RH, Wieboldt TF (2012) Compositional stability and diversity of vascular plant communities following logging disturbance in Appalachian forests. *Ecological Applications*, **22**, 502–516.

Brand FS, Jax K (2007) Focusing the meaning(s) of resilience: resilience as a descriptive concept and a boundary object. *Ecology and Society*, **12**, 23.

Brown PM, Kaufmann MR, Shepperd WD (1999) Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. *Landscape Ecology*, **14**, 513–532.

Bruelheide H, Luginbühl U (2009) Peeking at ecosystem stability: making use of a natural disturbance experiment to analyze resistance and resilience. *Ecology*, **90**, 1314–1325.

Crawford JA, Wahren CHA, Kyle S, Moir WH (2001) Responses of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. *Journal of Vegetation Science*, **12**, 261–268.

Dodge RS, Fulé PZ, Sieg CH (2008) Dalmatian toadflax (*Linaria dalmatica*) response to wildfire in a southwestern USA forest. *Ecoscience*, **15**, 213–222.

Doyle KM, Knight DH, Taylor DL, Barmore WJ, Benedict JM (1998) Seventeen years of forest succession following the Waterfalls Canyon Fire in Grand Teton National Park, Wyoming. *International Journal of Wildland Fire*, **8**, 45–55.

Falk DA, Heyerdahl EK, Brown PM *et al.* (2011) Multi-scale controls of historical forest-fire regimes: new insights from fire-scar networks. *Frontiers in Ecology and the Environment*, **9**, 446–454.

Folke C, Carpenter SR, Walker B, Scheffer M, Chapin T, Rockström J (2010) Resilience thinking: integrating resilience, adaptability and transformability. *Ecology and Society*, **15**, 20.

Fornwalt PJ, Kaufmann MR (2014) Understory plant community dynamics following a large, mixed severity wildfire in a *Pinus ponderosa – Pseudotsuga menziesii* forest, Colorado, USA. *Journal of Vegetation Science*, **25**, 805–818.

Fornwalt PJ, Kaufmann MR, Huckaby LS, Stoker JM, Stohlgren TJ (2003) Non-native plant invasions in managed and protected ponderosa pine/Douglas-fir forests of the Colorado Front Range. *Forest Ecology and Management*, **177**, 515–527.

Fornwalt PJ, Kaufmann MR, Huckaby LS, Stohlgren TJ (2009) Effects of past logging and grazing on understory plant communities in a montane Colorado forest. *Plant Ecology*, **203**, 99–109.

Fornwalt PJ, Kaufmann MR, Stohlgren TJ (2010) Impacts of mixed severity wildfire on exotic plants in a Colorado ponderosa pine-Douglas-fir forest. *Biological Invasions*, **12**, 2683–2695.

Foxx TS (1996) Vegetation succession after the La Mesa Fire at Bandelier National Monument. In: *Fire Effects in Southwestern Forests: Proceedings of the Second La Mesa Fire Symposium. Los Alamos, New Mexico, March 29–31, 1994, General Technical Report RM-286* (ed. Allen CD), pp. 47–69. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Freeman JP, Stohlgren TJ, Hunter ME, Omi PN, Martinson EJ, Chong GW, Brown CS (2007) Rapid assessment of postfire plant invasions in coniferous forests of the western United States. *Ecological Applications*, **17**, 1656–1665.

Fulé PZ, Crouse JE, Roccaforte JP, Kalies EL (2012) Do thinning and/or burning treatments in western USA ponderosa or Jeffrey pine-dominated forests help restore natural fire behavior? *Forest Ecology and Management*, **269**, 68–81.

Giglio L, Randerson JT, van der Werf GR (2013) Analysis of daily, monthly, and annual burned area using the fourth-generation global fire emissions database (GFED4). *Journal of Geophysical Research: Biogeosciences*, **118**, 1–12.

Graham RT, ed. (2003) *Hayman Fire Case Study*. General Technical Report RMRS-GTR-114. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.

Griffis KL, Crawford JA, Wagner MR, Moir WH (2001) Understory response to management treatments in northern Arizona ponderosa pine forests. *Forest Ecology and Management*, **146**, 239–245.

Haire SL, McGarigal K (2008) Inhabitants of landscape scars: succession of woody plants after large, severe forest fires in Arizona and New Mexico. *Southwestern Naturalist*, **53**, 141–161.

Haire SL, McGarigal K (2010) Effects of landscape patterns of fire severity on regenerating ponderosa pine forests (*Pinus ponderosa*) in New Mexico and Arizona, USA. *Landscape Ecology*, **25**, 1055–1069.

Halpern CB (1988) Early successional pathways and the resistance and resilience of forest communities. *Ecology*, **69**, 1703–1715.

Harrington HD (1964) *Manual of the Plants of Colorado*. Swallow Press, Chicago, IL.

Harvey BJ, Holzman BA (2014) Divergent successional pathways of stand development following fire in a California closed-cone pine forest. *Journal of Vegetation Science*, **25**, 88–99.

Hurteau MD, Stoddard MT, Fulé PZ (2011) The carbon costs of mitigating high-severity wildfire in southwestern ponderosa pine. *Global Change Biology*, **17**, 1516–1521.

Kaufmann MR, Regan CM, Brown PM (2000) Heterogeneity in ponderosa pine/Douglas-fir forests: age and size structure in unlogged and logged landscapes of central Colorado. *Canadian Journal of Forest Research*, **30**, 698–711.

Keane RE, Agee JK, Fulé P *et al.* (2008) Ecological effects of large fires on US landscapes: benefit or catastrophe? *International Journal of Wildland Fire*, **17**, 696–712.

Keyser TL, Lentile LB, Smith FW, Shepperd WD (2008) Changes in forest structure after a large, mixed-severity wildfire in ponderosa pine forests of the Black Hills, South Dakota, USA. *Forest Science*, **54**, 328–338.

Knox KJE, Clarke PJ (2012) Fire severity, feedback effects and resilience to alternative community states in forest assemblages. *Forest Ecology and Management*, **265**, 47–54.

Kuenzi AM, Fulé PZ, Sieg CH (2008) Effects of fire severity and pre-fire stand treatment on plant community recovery after a large wildfire. *Forest Ecology and Management*, **255**, 855–865.

Law BE, Hudiburg TW, Luyssaert S (2013) Thinning effects on forest productivity: consequences of preserving old forests and mitigating impacts of fire and drought. *Plant Ecology and Diversity*, **6**, 73–85.

Lin BB, Petersen B (2013) Resilience, regime shifts, and guided transition under climate change: examining the practical difficulties of managing continually changing systems. *Ecology and Society*, **18**, 28.

Lowe PO, Ffolliott PF, Dieterich JH, Patton DR (1978) *Determining Potential Wildlife Benefits from Wildfire in Arizona Ponderosa Pine Forests*. General Technical Report RM-52. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

McCune B, Mefford MJ (1999) *PC-ORD: Multivariate Analysis of Ecological Data. User's Guide*. MjM Software Design, Gleneden Beach, OR.

McGlone CM, Egan D (2009) The role of fire in the establishment and spread of nonnative plants in Arizona ponderosa pine forests: a review. *Journal of the Arizona-Nevada Academy of Science*, **41**, 75–86.

Merrill EH, Mayland HF, Peek JM (1980) Effects of a fall wildfire on herbaceous vegetation on xeric sites in the Selway-Bitterroot Wilderness, Idaho. *Journal of Range Management*, **33**, 363–367.

Moore R (1992) *Soil Survey of Pike National Forest, Eastern Part, Colorado, Parts of Douglas, El Paso, Jefferson, and Teller Counties*. U.S. Department of Agriculture, Forest Service, and Soil Conservation Service, U.S. Government Printing Office, Washington, DC.

NRCS [Natural Resources Conservation Service] (2013) *The PLANTS Database*. National Plant Data Center, Baton Rouge, LA. Available at: http://plants.usda.gov (accessed 4 December 2013).

Pearson HA, Davis JR, Schubert GH (1972) Effects of wildfire on timber and forage production in Arizona. *Journal of Range Management*, **25**, 250–253.

Prober SM, Thiele KR, Bramwell M (2007) Intense fires promote uncommon post-fire ephemerals in Currawang 'Acacia doratoxylon' dry scrubs of Little River Gorge, East Gippsland. *Victorian Naturalist*, **124**, 320–331.

Randerson JT, Chen Y, van der Werf GR, Rogers BM, Morton DC (2012) Global burned area and biomass burning emissions from small fires. *Journal of Geophysical Research*, **117**, G04012.

Rist L, Moen J (2013) Sustainability in forest management and a new role for resilience thinking. *Forest Ecology and Management*, **310**, 416–427.

Robichaud P, MacDonald L, Freeouf J, Neary D, Martin D, Ashmun L (2003) Postfire rehabilitation of the Hayman Fire. In: *Hayman Fire Case Study*, General Technical Report RMRS-GTR-114 (ed. Graham RT), pp. 293–313. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.

Savage M, Mast JN (2005) How resilient are southwestern ponderosa pine forests after crown fires? *Canadian Journal of Forest Research*, **35**, 967–977.

Savage M, Mast JN, Feddema JJ (2013) Double whammy: high-severity fire and drought in ponderosa pine forests of the Southwest. *Canadian Journal of Forest Research*, **43**, 570–583.

Sherriff RL, Veblen TT (2006) Ecological effects of changes in fire regimes in *Pinus ponderosa* ecosystems in the Colorado Front Range. *Journal of Vegetation Science*, **17**, 705–718.

Shive KL, Sieg CH, Fulé PZ (2013) Pre-wildfire management treatments interact with fire severity to have lasting effects on post-wildfire vegetation response. *Forest Ecology and Management*, **297**, 75–83.

Stohlgren TJ, Falkner MB, Schell LD (1995) A modified-Whittaker nested vegetation sampling method. *Vegetatio*, **117**, 113–121.

Stoy PC, Katul GG, Siqueira MBS *et al.* (2008) Role of vegetation in determining carbon sequestration along ecological succession in the southeastern United States. *Global Change Biology*, **14**, 1–19.

Swanson ME, Franklin JF, Beschta RL *et al.* (2011) The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment*, **9**, 117–125.

Turner MG, Romme WH, Gardner RH, Hargrove WW (1997) Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecological Monographs*, **67**, 411–433.

Weber WA, Wittmann RC (2001) *Colorado Flora: Eastern Slope*. University Press of Colorado, Niwot, CO.

Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increase western U.S. forest wildfire activity. *Science*, **313**, 940–943.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Location of burned and unburned plots in relation to the Hayman Fire and other large (>1000 ha) fires.

Fig. S2. Precipitation before and during the study period (left side axis), relative to the 1963–2012 long-term mean (dotted horizontal line), and vegetation variables (right-side axis) on the Hayman Fire, Colorado, USA. Vegetation variables are expressed as a proportion of their maximum value. Prefire vegetation data were collected in 1996/1997, the fire occurred in 2002, and postfire measurements were made starting in 2003. Precipitation data are from Manitou Experimental Forest, Woodland Park, Colorado.

Fig. S3. Successional vectors, standardized to the origin, illustrating trajectories of plant community change from prefire (1996/1997) conditions to (a) 1-year postfire, (b) 5-years, and (c) 10-years postfire following the 2002 Hayman Fire, Colorado, USA. Plots are displayed according to burn severity class. The lengths and directions of vectors are proportional to the magnitude and trajectory of change for each plot. Inset graphs show average (+1 SEM) deviance in multivariate space from prefire communities for each burn severity class, with larger means signifying greater amounts of change.