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# Predicting and mitigating weed invasions to restore natural post-fire succession in Mesa Verde National Park, Colorado, USA

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*Abstract.* Six large wildfires have burned in Mesa Verde National Park during the last 15 years, and extensive portions of burns were invaded by non-native plant species. The most threatening weed species include *Carduus nutans*, *Cirsium arvense*, and *Bromus tectorum*, and if untreated, they persist at least 13 years. We investigated patterns of weed distribution to identify plant communities most vulnerable to post-fire weed invasion and created a spatially explicit model to predict the most vulnerable sites. At the scale of the entire park, mature piñon–juniper woodlands growing on two soil series were most vulnerable to post-fire weed invasion; mountain shrublands were the least vulnerable. At a finer scale, greater richness of native species was correlated with greater numbers of non-native species, indicating that habitats with high native biodiversity are at the greatest risk of weed invasion. In unburned areas, weed density increased with greater soil nitrogen and phosphorus, and lower salinity. In burned areas weed density correlated with soil nitrogen status and textural class. We also evaluated the effectiveness of a variety of weed mitigation methods; aerial seeding of targeted high-risk areas with native grasses was the most effective treatment tested. We recommend a conservative mitigation plan using natives grass seed on only the most invasible sites.

*Additional keywords:* functional groups; invasive plants; native grasses; nutrient availability; piñon–juniper woodlands; soils.

## Introduction

Throughout history, fire has been a key ecological process in piñon–juniper woodlands and oak shrublands of the Colorado Plateau in the south-western United States. Prehistoric Ancestral Puebloans of the Mesa Verde region in south-western Colorado very likely used fires to clear woodlands and maintain agricultural fields (Wycoff 1977), and oral histories from long-time local residents describe intentional fires set by Ute Indians (M. Colyer, personal communication). It is unlikely however that human uses of fire were extensive or common enough to significantly alter fire dynamics in this region in contrast to some other areas of the south-western United States (Floyd *et al*. 2000; Allen 2002). Despite frequent lightning events in the summer monsoons, fires in Mesa Verde upland areas were characterized by numerous small, single-tree fires and large stand-replacing fires at intervals of decades or centuries (Floyd *et al*. 2000, 2004). Fire rotations of a century in the mountain shrublands and four or more centuries in the mature piñon–juniper woodlands have been documented in Mesa Verde and elsewhere in south-western Colorado (Floyd *et al*. 2000, 2004; Romme *et al*. 2003; Baker and Shinneman 2004; Eisenhart 2004;). These naturally long intervals between large fires allowed for development of extensive old-growth piñon–juniper woodlands (Romme *et al*. 2003; Baker and Shinneman 2004); coupled with exclusion of cattle grazing since $\sim$1930 in protected areas like Mesa Verde National Park (MVNP), these woodlands now support a rich understory flora highly valued for aesthetics and biodiversity (Austin 1999; Naillon *et al*. 1999; Floyd and Colyer 2003).

However, relative to this long fire interval of the preceding centuries, the frequency of large-scale fires has increased in the past two decades. This is in large part due to severe regional drought conditions preceded by wet climatic conditions that allowed for heavy fuel conditions, and coinciding with the natural end of a long fire cycle (Floyd *et al*. 2004). Six of those fires have occurred in just the last 15 years in Mesa Verde: the Long Mesa fire occurred in 1989, the Chapin 5 fire in 1996, Bircher and Pony fires in 2000, the Long Mesa 2 fire in 2001, and the Balcony Complex fire in 2003. Moreover, the current landscape differs from the past in floristic responses to the fires. Native plant species in some habitats of MVNP are now accompanied or largely replaced by a suite of recent arrivals, including *Carduus nutans* (musk thistle), *Cirsium arvense* (Canada thistle), *Lactuca serriola* (wire lettuce), *Bromus tectorum* (cheatgrass), *Salsola australis*

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(= *S. iberica* and *S. kali* [Russian thistle]), *Lappula redowskii* (stick seed), *Ranunculus testiculatus*, and *Alyssum parviflorum* (hoary alyssum). Thus, although the disturbance regime of this system apparently remains in the historical range of variability (Romme *et al.* 2003; Floyd *et al*. 2004), the recovery processes following fire have been dramatically altered from historic processes. Given the mandates to maintain natural ecological processes in MVNP as well as other natural areas (Swetnam *et al*. 1999; Allen *et al*. 2002), there is an urgent need to: (1) identify habitats most vulnerable to post-fire weed invasion; and (2) develop methods for restoring natural post-fire recovery processes in those habitats.

Post-fire restoration may, however, be problematic and overused (Keeley 2004), so in the present study we investigated landscape properties that determine 'invasibility' after fire to focus mitigation only on the most vulnerable habitats. Community stability, the life history of native and invasive species, soil fertility, and disturbance patterns are among those attributes that have been linked to invasibility (Grime 1998; Higgins *et al*. 1999; Levine 2000; McCann 2000; Prieur-Richard and Lavorel 2000; Dukes 2001; Hughes and Petchey 2001; Byers *et al*. 2002; With 2002). Recent studies contrast the role of species richness in either protecting communities against invasion, supporting the 'diversity–resistance hypothesis' originally proposed by Elton (Elton 1958; McCann 2000; Dukes 2001; Kennedy *et al*. 2002) or, conversely, other studies document a pattern of increasing invasibility with increasing species richness (Stohlgren *et al*. 1997, 2001, 2003; Higgins *et al*. 1999; Levine 2000). However, species richness alone cannot account for inter-community differences in invasibility (Davis *et al*. 2000; Prieur-Richard and Lavorel 2000; Prieur-Richard *et al*. 2002). Diversity and character of 'functional groups' have been deemed a more important deterrent of invasive plants because groups of species behave in similar fashion after fires (*viz*. prolific re-sprouting, weak re-sprouting, immediate germination, delayed germination), and ecological thresholds may be met in different ways by these different functions (Tilman *et al*. 1997; Tilman 1999; Lehman and Tilman 2000; Prieur-Richard and Lavorel 2000; Dukes 2001). We approached the invasive patterns at Mesa Verde by focusing on such 'functional groups' that categorize post-fire responses at both broad and fine spatial scales.

The role of disturbances, including fire, is of unequivocal importance in this debate (Prieur-Richard and Lavorel 2000), yet few studies address the relative importance of natives and invasives after wildfires (Keeley *et al*. 2003). Post-fire seeding efforts, although well-intentioned and widely used, have actually facilitated invasions in some situations by using non-native grass species (Robichaud *et al*. 2000; Keeley 2004). However, post-fire seeding with native grass species may be a way to prevent or reduce non-native invasions.

Post-fire patterns of native and non-native species are also influenced by changes in soil nutrients that accompany fires. In agricultural settings, it has long been recognized that growth and reproduction of invasive weedy species respond positively to increases in soil nutrient availability, particularly to nitrogen (Mohler 2001). Nutrient availability has more recently been established as one of the key ecosystem attributes that determine the invasibility of native ecosystems by non-native plant species (Vitousek 1990). Davis *et al*. (2000) further suggested that an important mechanism of ecosystem invasibility is related to the pulsing of resource availability (such as nutrients). Two of the species of concern in Mesa Verde, *Carduus nutans* and *Cirsium arvense*, have shown increased production with increased nutrients in mixed species experiments (Austin *et al*. 1985). However, responses to nutrients are complex; *Cirsium arvense* shoot density decreased with experimental nutrient application when subjected to intense inter-specific competition (Edwards *et al*. 2000). Grasslands, forests, woodlands, and chaparral ecosystems of the arid South-west USA and other arid regions characteristically demonstrate great fluctuations in nutrient availability following fires (DeLuca and Zouhar 2000; Castelli and Lazzari 2002). Between disturbance events, these ecosystems typically maintain low levels of soil organic matter and in turn nitrogen availability. Moreover, the alkaline status of many arid-land soils results in the majority of soil phosphorus being held in unavailable calcium phosphate forms (Balba 1995). Various investigators have found relationships between soil nutrient status and invasive weed diversity and abundance in arid ecosystems (Bashkin *et al*. 2003).

In the present study, we considered both the possible role of disturbances created by large wildfires in invasibility in a semi-arid woodland ecosystem in south-western Colorado and the impact of the invasions on biodiversity in early post-fire succession. We also assessed the effectiveness of various post-fire mitigation treatments. Although we focused on MVNP, our results are broadly applicable to much of the Colorado Plateau in western Colorado, eastern Utah, north-eastern Arizona, and north-western New Mexico, and the general principles are relevant to many post-fire restoration projects.

We addressed the following questions:

- What is the association between native and non-native plant diversity in burned and unburned landscapes in Mesa Verde?
- Do characteristics of functional groups (relative abundance of sprouting *v.* non-sprouting species) in the pre-fire community influence invasion pattern?
- What is the contribution of microhabitat differences in soil series, texture, and chemical properties to invasibility?
- How can we model invasibility after fire in an effort to focus restoration only on the most vulnerable habitats?
- How effective are aerial seeding of native grasses, and mechanical and chemical treatments in preventing non-native invasions?

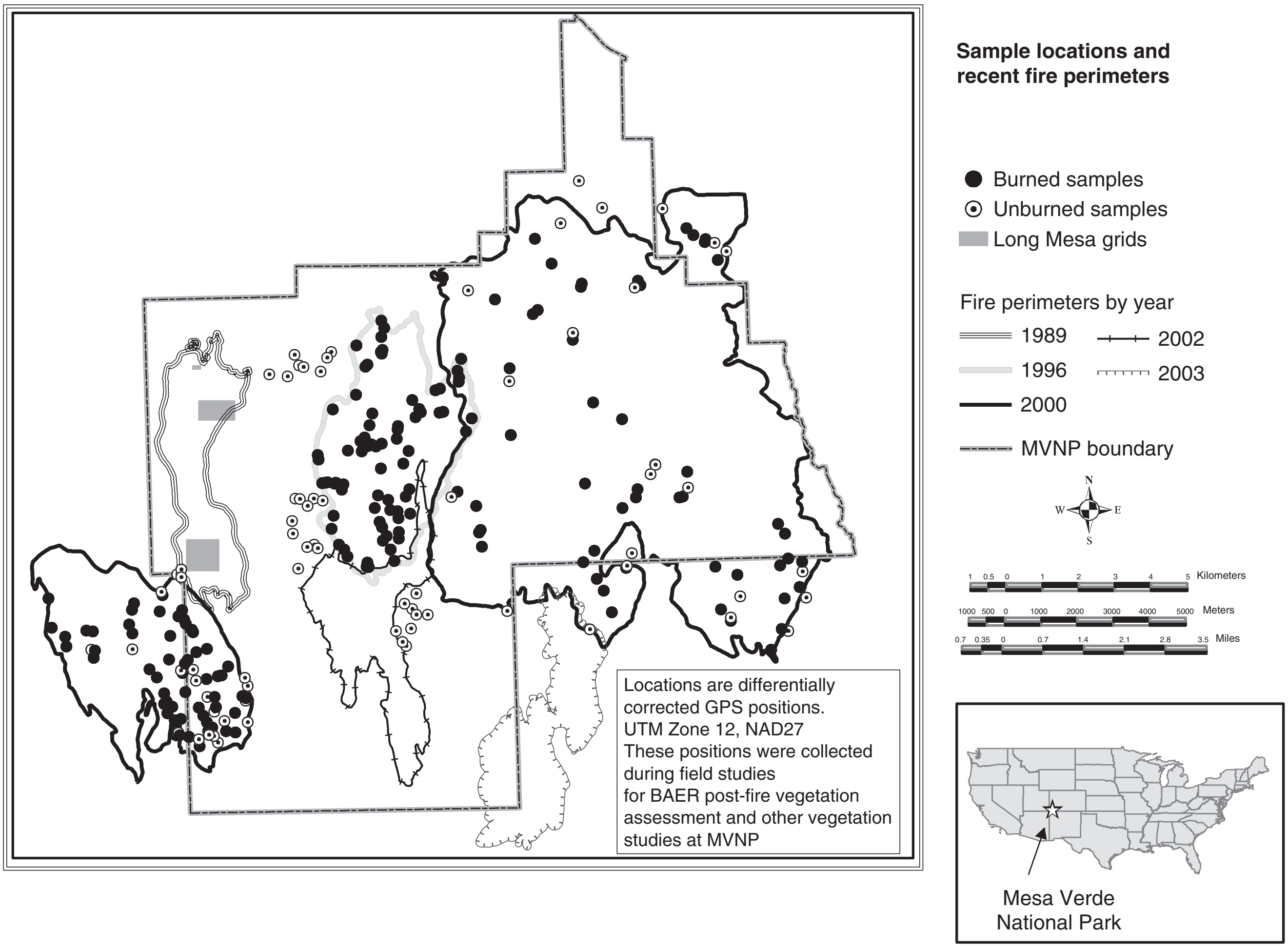


**Fig. 1.** Recent fires on Mesa Verde cuesta and sampling locations in the 1989 Long Mesa, 1996 Chapin 5, and 2000 Bircher and Pony fires.

## Study area and recent fire history

Mesa Verde National Park (MVNP) is located in the south-western corner of Colorado, USA (Fig. 1). The national park occupies the middle of a prominent cuesta (a landform with a long, gentle slope formed by caprock and a short steep slope on eroded edges) that slopes from 2060 m in the south to 2485 m in the north. The surrounding area, roughly one-half of the cuesta, is Ute Mountain Ute Tribal Land. The south and eastern edges of the cuesta are bordered by the Mancos River, whereas steep escarpments characterize the north. The cuesta is composed of Cretaceous sandstones and shales.

Two major vegetation types cover most of MVNP. *Pinus edulis* (piñon pine) and *Juniperus osteosperma* (Utah juniper), hereafter called piñon–juniper woodlands, dominate the lower elevations of the mesa tops and canyon slopes. Piñon–juniper woodlands in Mesa Verde tend to be old and structurally diverse. *Purshia tridentata* (bitterbrush) is often the dominant understory shrub. Other species may include low densities of *Artemisia tridentata* (big sagebrush), *Peraphyllum ramossisium* (squawapple), *Quercus gambelii* (Gambel oak), *Amelanchier utahensis* (Utah serviceberry), and *Fendlera rupicola* (fendler bush). Common forbs include *Penstemon linearoides*, *Pedicularis centranthera*, *Cryptantha bakerii*, *Polyonum sawatchensis*, *Lupinus ammophila*, *Astragalus scopulorum*, *Commandra umbellata*, *Cymopterus bulbosus*, *C. purpurescens*, and *Yucca baccata*. The dominant understory grass is *Poa fendleriana* (mutton grass) (Naillon *et al*. 1999; Floyd and Colyer 2003). Dominant species in these piñon–juniper communities typically do not re-sprout vigorously after fire, and therefore we have grouped the piñon–juniper types into a ‘non-sprouting’ functional group.

Mountain shrublands are found at the upper elevations on Mesa Verde and are dominated by dense stands of *Quercus gambelii*, *Amelanchier utahensis*, *Peraphyllum ramossisium*, and *Fendlera rupicola*. Common forbs include *Lomatium dissectum*, *Delphinium nelsonii*, and *Lathrys pauciflorus*. Grasses include *Stipa comata* (= *Heterostipa comata*), *Koeleria macrantha* (= *K. cristata*) and *Agroypyron smithii* (= *Pascopyron smithii*) (Weber and Wittmann 1999). These species re-sprout vigorously after fires, distinguishing this 'sprouting' functional group from the piñon–juniper types. Less common but locally important vegetation types also included in this functional group include Douglas-fir forests, meadows, sagebrush–grasslands and riparian areas.

In the present study, we focused on patterns following three recent fires. The 1989 Long Mesa Fire began with a lightning strike and burned 1800 ha of mesa-top, deep canyons, and steep north-facing habitats, with old-growth piñon–juniper, mountain shrublands, sagebrush, and Douglas-fir vegetation. No mitigation treatments were applied after this fire. The Chapin 5 fire in August 1996 burned 1972 ha, impacting seven vegetation types including those listed above and wet meadows. Under Department of Interior Burned Area Emergency Rehabilitation (BAER) funding, mitigation treatments – aerial seeding, herbicide, and mechanical – were applied. The Bircher fire burned 10 592 ha in late July 2000, including piñon–juniper woodlands of varying stages of succession, mountain shrublands, open wet meadows, and riparian communities. A few weeks later, the Pony Fire burned 2272 ha, affecting large tracts of old-growth piñon–juniper woodlands. In both fires, helicopter application of mixes of four to seven native grass species took place under the BAER program.

## Methods

Because large fires occur unpredictably, our post-fire sampling was necessarily opportunistic. Funding sources and amounts were also variable, so methods differed somewhat following each of the three large fires. However, all of the methods and results were directed at two key topics: predicting invasibility and evaluating mitigation effectiveness.

### *Predicting highly invasible habitats after fire*

#### *Long Mesa 1989 fire*

Two sampling grids were established in 1991 to include the range of pre-fire vegetation on Long Mesa and within Long Canyon in western MVNP (Fig. 1). The 'southern grid' consisted of a square kilometer, sampled systematically every 100 m, for a total of 121 sampling points. This grid represented the heterogeneity of vegetation within the piñon–juniper woodland and shrubland mosaic that characterizes low to middle elevations in MVNP. The 'northern grid' was placed within the essentially treeless, mountain shrub community, which extends over much of the northern, higher elevation, sector of MVNP. As the vegetation was relatively homogeneous, the size was reduced to 1 km by 0.6 km and the number of sampling points to 66. All points were severely burned. 'Control points' consisted of nearby vegetation missed by the 1989 fire. Initial post-fire patterns were documented in 1991–1993; at each point, releve analyses listed the Braun-Blanquet cover/abundance of each plant species (Mueller-Dombois and Ellenberg 2002), and the density of each non-native species was determined in 314 $m^2$ plots. The plots were revisited in 2002 to evaluate the persistence of non-native invasive plants and their effects on the density and abundance of native species (not shown here); owing to extreme drought conditions and low plant cover, we simply recorded presence or absence of each invasive species within a 10 m radius of the point. Data were analyzed statistically using the Statistical Package for the Social Sciences (SPSS, Chicago, IL, USA); the density of non-native plants (in 1993) and the presence of non-native species (in 2002) were each compared statistically across burned and unburned treatments using a Student's *t*-test (Sokal and Rohlf 1981).

#### *Chapin 5 1996 fire*

The Chapin 5 fire was separated into 19 'habitats' by stratifying vegetation communities, substrates, and slope categories in the GIS software IDRISI (Clark Labs, Worcester, MA, USA). Random sample locations were created within each habitat. Eighty burned points were sampled in 1997, 1998, and 1999 under the Burn Area Emergency Rehabilitation (BAER) program; in 2003, we added 25 unburned control points with similar site characteristics to burned points. We re-visited all 105 points in 2003 to evaluate long-term trends in native and invasive plant distributions. At each point, the density of each non-native plant species that was singly rooted was counted in each of three 314 $m^2$ plots. The density of highly abundant grasses, such as *Bromus tectorum* was estimated within each plot. In 2003, although a drought prevailed in the area, adequate precipitation in May and June allowed for germination of many forbs, and we recorded the density of each invasive species at each point, in 314-$m^2$ plots. Analysis of Variance (ANOVA) tests were run to detect significant differences in the density of invasive plants across habitat types, grouped into non-sprouting (piñon–juniper), prolifically sprouting (mountain shrubland) and weakly sprouting (riparian) functional groups (Sokal and Rohlf 1981).

#### *Bircher and Pony 2000 fires*

One hundred twenty points were randomly identified using a 'sample' procedure in the GIS software IDRISI and grouped into 40 triplicate sampling units; (1) an unburned control point of similar slope, aspect, pre-fire vegetation and geologic substrate was grouped with (2) a burned point that was not treated; and (3) a burned point that was treated with native grasses, as described below (Fig. 1). (Note: the treated burned points are not considered in the present analysis; they are used in a later experiment to evaluate the success of mitigation.) In 2002 and 2003, native and invasive species diversity was assessed using the 'Modified-Whitaker' system of embedded small and large, multi-scale (1, 10, 100, and 1000 $m^2$) plots (Stohlgren *et al.* 1997). We recorded the number of native and non-native species in each plot as well as the cover of each species in the ten 1 $m^2$ plots (Stohlgren *et al.* 1997). We returned to each point in 2003 and recorded the density of each singly-rooted non-native species in three 314 $m^2$

plots. *Bromus tectorum* density was estimated. The densities of native and non-native species were subjected to Pearson correlation analyses (Sokal and Rohlf 1981; Stohlgren *et al*. 2003).

We sampled soils in the same paired burned and unburned samples (again eliminating the seeded plots) in the Bircher and Pony fires of 2000. Soil chemical analyses were conducted on soils collected in 2002 and 2003, whereas soil physical properties were measured only on soils collected in 2002. Twenty soil cores were extracted to a depth of 5 cm and then aggregated into one bulk sample. Soil samples were put on ice in the field and 10 g subsamples were extracted within 12 h with 2 M KCl and analyzed for nitrate and exchangeable ammonium using an autoanalyzer. Duplicate 10 g soil samples were incubated in a hydrated state for ~3 weeks and then extracted in the same manner for nitrate and ammonium to estimate potential nitrogen mineralization (Binkley and Vitousek 1991). Organic matter was estimated by pre-treating samples with concentrated HCl to eliminate carbonate, i.e. inorganic carbon. This was followed by ignition at 550°C, and loss of organic material was calculated. Soil pH was measured electrometrically in a 2 : 1 water : soil ratio. Soil available phosphorus was measured using an anion exchange resin extraction and analyzed colorimetrically (Lajtha *et al.* 1999). Soluble salts were determined by electrical conductivity following the protocol of Janzen (1993). Texture was measured by hydrometer (Sheldrick and Wang 1993) and water content was measured gravimetrically. Student's *t*-tests were run to detect significant differences in each soil property between burned and unburned soils. We also correlated each soil property with the density of invasive plants using Pearson correlation analysis (Sokal and Rohlf 1981).

### *Developing a weed-risk model*

Each soil series and each vegetation community was ranked using an ordinal scale of 1–3, representing low to high density of invasive non-native species, based on the soil analyses described below. These ranked maps were then combined using a linear weighted combination technique in ArcView GIS 3.3 (Environmental Systems Research Institute, Redlands, CA, USA), creating a spatially explicit 'index of invasiblity'. Soil series information was extracted using GIS for the sample points in the 1996 and 2000 fires. An ordinal variable (1 = low, 2 = intermediate, 3 = high) based on the mean density of invasive plants for that series (see below) was assigned to define invasibility of each soil series. Unsampled soil series were also assigned an invasibility class depending on the Natural Resource Conservation Service (NRCS) published chemical information (those with chemistry and texture similar to sampled soil classes were grouped in a similar susceptibility class). All MVNP and surrounding vegetation communities were similarly classified (low to high susceptibility) based on relative cover of sprouting species, defining their 'functional groups'. Spatial data layers were created for susceptibility due to vegetation and susceptibility due to soils. To determine the most appropriate contribution of each parameter, we developed a sensitivity analysis in which the relative weighting of soil or vegetation characteristics was varied (70–30, 60–40, or 50–50%). The map resulting from each combination was overlain on the current weed distribution in Mesa Verde to determine the weighting that provided most accurate descriptions of weed patterns. The best representation of Mesa Verde was approached when vegetation was weighted at 70% and susceptibility due to soil fertility at 30%; therefore these weightings were used to develop the spatially explicit weed-risk map for the cuesta.

### *Evaluating effectiveness of post-fire mitigation*

The BAER program evaluated the damages immediately after the 1996 Chapin 5 fire and recommended mitigation treatments to reduce erosion and prevent or lessen impacts to native vegetation recovery by noxious non-native invasion (Robichaud *et al*. 2000; Floyd *et al*. 2001). In October 1996, 200 acres (80 ha) of Park Mesa, an old-growth piñon–juniper woodland deemed at 'high-risk' of invasion by non-native species, was seeded by helicopter application with mixes of native grass seeds. Seed mixes varied by locality; they consisted of local varieties of *Poa fendleriana* (mutton grass), *Stipa comata* (= *Heterostipa comata*, needle and thread grass), *Agropyron smithii* (= *Elymus smithii*, western wheat), *A. trachycaulon* (= *Elymus trachycaulus*, slender wheat), *Oryzopsis hymenoides* (Indian ricegrass), *Koeleria macrantha* (= *Koeleria cristata*, junegrass) and *Sitanion hystrix* (= *Elymus elymoides*, squirrel tail grass) (Weber and Wittmann 1999) at total rates of 3.4–5 kg $ha^{-1}$. Stands of *Cirsium arvense* also were located with GPS on Park Mesa and sprayed with herbicide (3,6-dichloro-2-pyridinecarboxylic acid, monoethanolamine salt 7.5%; 2,4-dichlorophenoxyacetic acid, tris-propanolamine salt 38.4%) mixed with JLB oil plus IFA-S90 Surfactant (DOW Agrosciences, Indianapolis, IN, USA). 'Before' and 'after' photographs were taken of each treatment site. After one year, an additional spraying took place on stands that had >20% cover. Mechanical removal of *Carduus nutans* plants took place during the first growing season after the fire in selected high density stands.

To determine effectiveness of the aerial seeding, in addition to the monitoring of the Chapin 5 fire described above, a series of plots of similar vegetation, slope, aspect and substrate was established on Park Mesa in 25 triplicate groupings: (1) seeded with native grasses; (2) burned but not treated; and (3) controls. Plots were sampled in 1998, 1999, 2001, and 2003. At each point, the density of each seeded grass and non-native plant species that was singly rooted was counted in each of three 314 $m^2$ plots. The density of highly abundant grasses, such as *Bromus tectorum*, was estimated within each plot.

A similar aerial seeding mitigation was carried out in 'high-risk' areas after the Bircher and Pony fires of 2000. In addition to the grasses listed above, some mixes included *Bouteloua gracilis* and *Sporobolus cryptandrus*. To determine the impact of the mitigation treatments on weed invasion, we sampled the same 120 plots described above for the Bircher and Pony fires: (1) an unburned control point of similar slope, aspect, pre-fire vegetation and geologic substrate was grouped with (2) a burned point that was not treated; and (3) a burned point that was treated with native grasses. Analysis of Variance (ANOVA) tests were run on 2002 and 2003 data; the density of plants of each invasive species was compared between the three treatments. The density of invasive plants was correlated with soil properties described with Pearson correlation analysis (Sokal and Rohlf 1981).

## Results

### *Defining characteristics of invasible habitats after fire*

#### *Native and invasive diversity patterns*

In 1000 $m^2$ plots, a strong positive correlation coefficient suggests that habitats supporting greater numbers of native species also maintain a richer non-native flora (Table 1). This relationship held true in both 40 recently burned areas ($r = 0.42$, $P < 0.05$) and in 40 paired nearby unburned areas ($r = 0.74$, $P < 0.05$).

#### *Role of sprouting species in invasions*

Collectively, although variable in understory shrubs and forbs, the piñon–juniper woodlands in MVNP represent a functional type that lacks abundant perennial sprouters. Mountain shrubland vegetation represents a functional type characterized by prolific sprouting shrub species. Meadows and wetlands have many sprouting grasses or sedges and, therefore, they are grouped together. Eight years after the Chapin 5 fire, there were significantly fewer invasive plants in the functional groups characterized by sprouting perennial shrubs or graminoids; the functional group lacking abundant re-sprouting species was the most vulnerable to invasion (Table 2).

#### *Trends in non-native invasions 3 years after fire*

In 2003, there was significantly greater density of invasive plants in burned plots relative to paired unburned plots in the 2000 Bircher and Pony fires (Table 3). Major invasive species included *Carduus nutans*, *Cirsium arvense*, *Lactuca serriola*, and *Salsola australis*. Also, *Bromus tectorum* expanded rapidly from small foci within the park and the region as a whole.

#### *Trends in non-native invasions 8 years after fire*

Eight years after the 1996 Chapin 5 fire, there was a significant difference in the density of invasive species, comparing unburned and burned habitats (Table 4). The most aggressive and persistent invasive species was *Carduus nutans*. There was also significantly greater density of *Bromus tectorum* detected in burned habitats (Table 4).

#### *Trends in non-native invasions 13 years after fire*

Thirteen years after the 1989 Long Mesa fire (in 2002), severe drought conditions reduced growth throughout the area, so we simply recorded the presence and absence of native and non-native species rather than cover or density.

**Table 1. Correlation analyses of the number of native and non-native species among the plot sizes used in 'Modified-Whitaker' sampling, Mesa Verde National Park**

Significance values are given for *t*-tests associated with the Pearson correlation coefficient

| Plot size ($m^2$) | Correlation coefficient ($r$) | $P$-value | $n$ |
|---|---|---|---|
| 1 | −0.042 | >0.05 | 619 |
| 10 | −0.026 | >0.05 | 123 |
| 100 | 0.324 | 0.01 | 60 |
| 1000 | 0.534 | <0.01 | 54 |

**Table 2. The density (number per 314 $m^2$) of non-native plants in various burned habitats classed by functional group**

Data were collected in 2003, 8 years after the Chapin 5 fire. Data are: mean, standard error. $F = 3.9$, $P = 0.02$, significant difference in non-native density across functional groups

| Community types | Prevalence of sprouting shrubs | Non-native density | Sample size |
|---|---|---|---|
| Piñon–juniper | Non-sprouters | 1008.2, 296.7 | 67 |
| Mountain shrubland | Prolific sprouters | 8.7, 3.8 | 44 |
| Riparian | Sprouting grasses | 24.0, 24.0 | 3 |

**Table 3. The density (number per 314 $m^2$) of non-native invasive plants, primarily *Carduus nutans* and *Cirsium arvense*, 3 years after the 2000 Bircher and Pony fires**

Data were collected in 2003 after less than normal precipitation conditions. Values given are mean, standard error. $F = 3.0$, $P = 0.05$, significant difference in non-native density across three treatments

| Treatment | Non-native density | Sample size |
|---|---|---|
| Unburned | 37.5, 22.9 | 40 |
| Burned | 724.3, 361 | 40 |

**Table 4. The density (number per 314 $m^2$) of non-native plants, primarily *Carduus nutans* and *Cirsium arvense*, in 2003, 8 years after the 1996 Chapin 5 fire**

The estimated density of *Bromus tectorum* is shown separately. Data are: mean, standard error

| Treatment | Non-native plant density (excluding *Bromus tectorum*) | *Bromus tectorum* | Sample size |
|---|---|---|---|
| Unburned | 0.58, 0.29 | 0.08, 0.28 | 48 |
| Burned | 21.9, 5.3 | 574.6, 178 | 114 |
| Significance | $F = 6.7$, $P = 0.01$ | $F = 4.8$, $P = 0.038$ | |

Whereas the number of native species was not significantly different between sprouting and non-sprouting functional groups, there was a significant difference in the diversity of invasive species; there is significantly greater diversity in the invasive flora in the sites lacking vigorously sprouting shrubs and grasses that persists for at least 13 years (Table 5).

### *Soil chemistry and invasibility*

As suggested by the large standard errors in Tables 2–4, some sites within the burned, non-sprouting functional groups were invaded whereas others remained free of non-natives. Ash and organic matter inputs following the Bircher and Pony fires of 2000 significantly increased soil pH, salinity (electrical conductivity), and the availability of nitrogen and phosphorus. As a whole, these findings reflect that combustion of plant materials results in rapid mineralization and release of base-forming cations and other essential plant nutrients. The drought conditions that persisted at Mesa Verde between the fire season of 2000 and when the soils were sampled in 2002 prevented leaching of fire-released salts and nutrients. The winter of 2002–2003 was considerably wetter, which likely explains why there were fewer significant differences between severely burned and unburned soil characteristics measured during the following spring (Table 6). Although we measured numerous soil attributes that were altered by fire, non-native densities within the actual burned areas only correlated weakly with variation in soil nitrate (Table 6). Non-native densities in burned areas were also found to correlate with percentage silt, which did not vary as a function of burning. Interestingly, in unburned sites, although non-native densities were considerably lower than in burned sites (Table 7), their distribution did correlate strongly with soil available phosphorus and weakly with net nitrogen mineralization and salinity.

### *Extrapolation to NRCS soil mapping units*

There was a significant difference in the density of non-natives (excluding *Bromus tectorum*) across seven soil series defined by the USDA-NRCS soil maps in the Bircher and Pony fires ($F = 3.9$, $P = 0.004$). These data (Fig. 2*a*) suggest that within the piñon–juniper habitat, Mikim loam and Arabrab-Longburn soils are most invasible after the soils are burned. These findings were apparently not simply due to percentage silt or available nitrate as these soil attributes were not significantly greater than less susceptible soils in the area. However, burned Mikim soils were significantly higher in phosphorus than other soils sampled (available phosphorus in Mikim samples averaged 75 $\mu$g gdw$^{-1}$ soil whereas the overall mean available phosphorus was 49 $\mu$g gdw$^{-1}$ soil);

**Table 5. The number of native and invasive species recorded in sample plots classed by functional group (piñon–juniper lacking prolific sprouting species) and mountain shrubland (prolific post-fire sprouting) in the Long Mesa fire 13 years after fire**

Data were collected under extreme drought conditions in 2002. Data are: mean, standard error

| Type | Sprouting functional group | Non-sprouting functional group | Statistical significance |
|---|---|---|---|
| Native species | 14.6, 3.6 | 16.4, 4.3 | n.s. |
| Non-native species | 0.4, 0.6 | 2.2, 1.2 | $t = 5.3$, $P < 0.01$ |
| Sample size | 29 | 45 | |

**Table 7. Correlations significant at the probability < 0.10 level in unburned and post-fire soil properties with non-native densities**

Sample size = 57, data shown are for 2002. Significance values are given for *t*-tests associated with the Pearson correlation coefficient

| Property | Pearson correlation coefficient ($r$) | $P$-value |
|---|---|---|
| Unburned | | |
| Net nitrogen mineralization | 0.43 | 0.01 |
| Available phosphorus ($\mu$g gdw$^{-1}$ soil) | 0.56 | 0.01 |
| Conductivity (dS m$^{-1}$) | −0.40 | 0.01 |
| Post-fire | | |
| Available nitrate (mg gdw$^{-1}$ soil) | 0.26 | 0.06 |
| Percentage silt | 0.29 | 0.08 |

**Table 6. Soil properties that were significantly different in burned and unburned sites 2 and 3 years following the Mesa Verde Bircher and Pony fires**

Values in parentheses are standard errors. Differences between the mean weed density in burned and unburned samples were tested with *t*-tests; probability values associated with those tests are shown

| Property | Unburned | Burned | $P$-value |
|---|---|---|---|
| 2 years after fire | | | |
| Available nitrogen $NO_3^-$ and $NH_4^+$ (mg gdw$^{-1}$ soil) | 27 (8) | 61 (5) | 0.001 |
| Available phosphorus ($\mu$g gdw$^{-1}$ soil) | 32 (7) | 50 (5) | 0.03 |
| pH | 6 | 6.4 | 0.003 |
| Conductivity (dS m$^{-1}$) | 0.19 (0.03) | 0.36 (0.02) | <0.001 |
| % soil water | 3.1 (0.3) | 2.1 (0.2) | 0.003 |
| 3 years after fire | | | |
| Available phosphorus ($\mu$g gdw$^{-1}$ soil) | 28 (4) | 45 (5) | 0.02 |
| Conductivity (dS m$^{-1}$) | 0.11 (0.01) | 0.18 (0.01) | <0.001 |

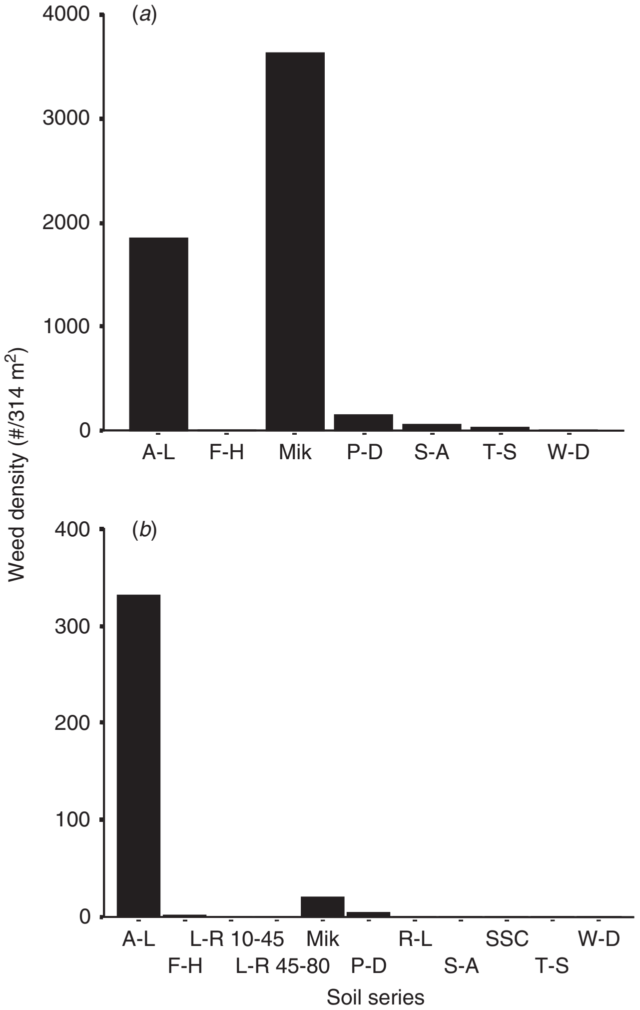


**Fig. 2.** Mean density of invasive species, excluding cheatgrass (*Bromus tectorum*), across soil series, defined by the Natural Resource Conservation Service in Mesa Verde National Park. (*a*) Density of weeds in soils burned in the 2000 Bircher and Pony fires. (*b*) Density of weeds in nearby unburned plots. The density of weeds is greatest in Arabrab-Longhorn and Mikim soils in both the burned and unburned conditions; scales vary because the density of weeds in burned soils (*a*) is much greater than in unburned soils (*b*). Note that in some cases, paired plots were different soil series, therefore L-R, P-D, and SSC types are not represented in part (*a*) and appear in part (*b*). A-L, Arabrab-Longhorn; F-H, Fughes-Herm Complex; L-R, Longburn Rock Outcrop 10-45, 45-80; Mik, Mikim Loam; P-D, Prater-Dolcan Complex 25-60; R-L, Roubideau Loam 1-6; S-A, Sheek-Archuleta Rock Outcrop; SSC, Sideshow Silty Clay Loam 6-12; T-S, Tragmon-Sheek Complex 12-25; W-D, Wauquie-Dolcan Rock Complex 25-80.

this trend does not apply to Arabrab-Longburn soils, which were low in available phosphorus (average 27 $\mu$g gdw$^{-1}$ soil). Whereas no significant difference in non-natives was detected across unburned USDA-NRCS soil series ($F = 1.5$, $P > 0.05$), Fig. 2*b* suggests that the Arabrab-Longburn soils likely support non-natives even when unburned.

### *Weed risk model*

Using the vulnerability of different vegetation and soil series after the 1996 and 2000 fires (described above), we developed a spatial model representing areas at risk of future invasion by non-natives after fires (Fig. 3). Approximately 35% (7512 ha) of MVNP was classed as 'high-risk' from post-fire invasive species and 19% (4055 ha) at moderate risk from invasive species. The at-risk areas occur primarily on the southern portions of the park, where most of the old-growth piñon–juniper woodlands dominate, and which support the most vulnerable soils types, Mikim loam and Arabrab-Longburn. Using this spatial model (Fig. 3), resource managers can identify the areas most vulnerable to future weed infestation after fire; these are the likely areas where post-fire mitigation will be most beneficial.

## *Effectiveness of mitigation treatments on invasive species*

### *Aerial seeding with native grasses*

*Carduus nutans* was the most abundant non-native species after the 1996 fire and was the focus of monitoring. For the first 8 years after a conservative restoration program that involved seeding with native grasses, there were significantly fewer *Carduus nutans* in seeded than in paired burned but unseeded treatments. Invasive plants were not eliminated from treated areas, but their densities were significantly reduced (Table 8). There were significantly more native grasses in the seeded plots (mean = 802 per 314 m$^2$, s.e. = 49) when compared with paired unseeded plots (mean = 7 per 314 m$^2$, s.e. = 1, $F = 4.6$, $P < 0.03$). The seeded treatments also had a more diverse native grass flora than unseeded areas. Whereas the unseeded areas contained sparse native *Poa fendleriana* and *Stipa comata* (= *Heterostipa comata*), seeded treatments supported *Stipa comata*, *Agropyron smithii* (= *Elymus smithii*), *A. trachycaulon* (= *Elymus trachycaulus*), *Poa fendleriana*, *Oryzopsis hymenoides* and *Sitanion hystrix* (= *Elymus elymoides*). In a related study, we found no significant difference in diversity and density of native forbs in seeded and untreated plots, suggesting that treatments do not prevent native succession (M.L. Floyd, unpublished data).

One of the most alarming invasive species in Mesa Verde in 2003 was *Bromus tectorum*. Whereas it was present at 5% of sample points 3 years after the 1996 Chapin 5 fire, it expanded greatly in 2003. *Bromus tectorum* was more plentiful in burned than unburned areas (Table 4); however we were unable to detect a statistical difference in *Bromus tectorum* density between untreated burned (mean = 16 913 plants per hectare, s.e. = 3962) and burned seeded treatments on Park Mesa (mean = 9500 plants per hectare, s.e. = 2853, $F = 2.3$, $P = 0.14$). Therefore, seeding mitigation has not prevented the spread of *Bromus tectorum* within burned areas.

*Salsola autralis* and *Lactuca serriola*, both prolific invasives in 1997 and 1998, had virtually disappeared from the

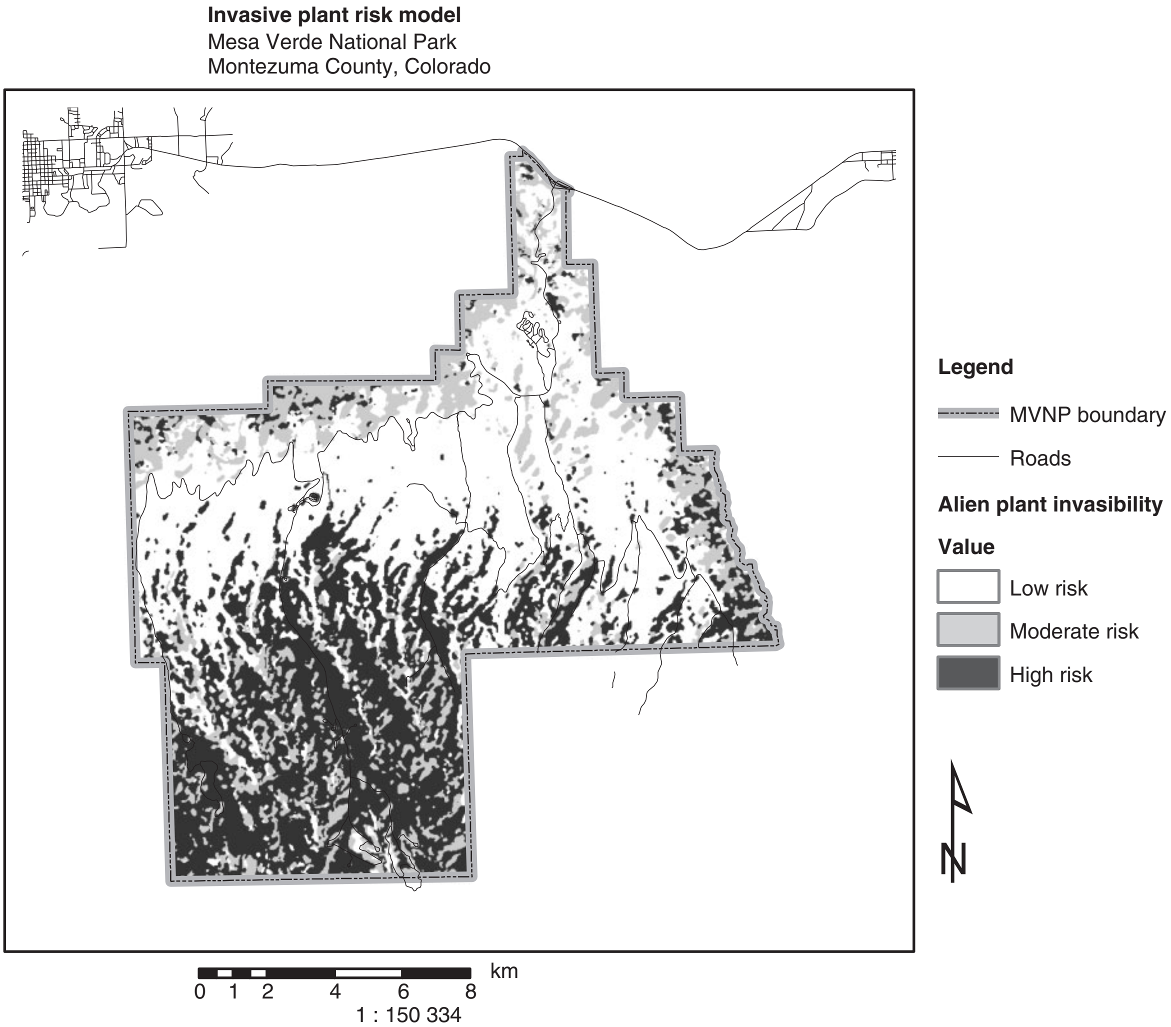


**Fig. 3.** Weed risk map of Mesa Verde National Park.

burned landscape by 2003. Other invasives, such as *Lappula redowski* and *Alyssum parviflorum* were present in 1997 and 1998, but also were only sporadically found in 2003.

### *Herbicide treatments*

Large patches of *Cirsium arvense* in the upland areas of the Chapin 5 fire were treated with herbicide in 1997 and 1998. We estimated the cover and photographed each of the upland stands 'before' and 1 year 'after' herbicide treatment. In 2003, 6 years after treatment, matched pre-treatment photographs and field visits demonstrated that this treatment was extremely effective. All of the *Cirsium arvense* was dead in five of the seven sites; in two sites, only one or two plants remained.

### *Mechanical treatments*

Mechanical treatments took place during the first year after the 1996 Chapin 5 fire, either along roadsides or in isolated patches. *Carduus nutans* seed heads were removed and individual plants were dug out. Where native grasses such as the rhizomatous *Agropyron smithii* were part of the post-fire successional vegetation, this treatment was highly effective; in 2003, we established 10 plots throughout this area and no *Carduus nutans* plants were detected. However, in 10 plots lacking grasses, this treatment was not effective; stands of

**Table 8. Comparison of non-native plant density (number per hectare) in burned seeded and unseeded treatments of Park Mesa, Chapin 5 fire, Mesa Verde National Park**
Data are: mean ± standard deviation

| Year of monitoring | Unseeded control | Seeded treatment[a] | No. plots |
|---|---|---|---|
| 1998 | 8000 ± 728 | 576 ± 602 | 50 |
| 1999 | 13 373 ± 9301 | 1779 ± 65 | 50 |
| 2001 | 6125 ± 1138 | 3230 ± 5933 | 26 |
| 2003 | 3596 ± 7515 | 928 ± 1680 | 195 |

[a]ANOVA analyses for each year demonstrate significant differences ($P < 0.05$) between seeded and unseeded burned areas.

*Carduus nutans* persisted in 2003 (average $117 \pm 452$ plants per $100\,m^2$).

## Discussion

Six large, severe fires have burned tens of thousands of hectares in Mesa Verde National Park (MVNP) and surrounding landscapes during the last 15 years, and extensive portions of those burned areas have been invaded by non-native plant species. Fire and weed invasion are primary management concerns not just in MVNP, but in similar piñon–juniper and mountain shrubland vegetation types throughout the Colorado Plateau. Aggressive non-native species may competitively displace native species, including endemics and others of limited geographic distribution, and may alter fundamental ecosystem processes such as biogeochemical cycling, plant competitive interactions, and disturbance regimes. The potentially most threatening weed species in MVNP – the ones of greatest management concern – include *Carduus nutans*, *Cirsium arvense*, and *Bromus tectorum*. In the present study, we investigated the patterns and processes of weed invasion following the 1989, 1996, and 2000 fires in MVNP to identify the kinds of plant communities and soil series that are most vulnerable to post-fire weed invasion and to evaluate the effectiveness of a variety of weed mitigation methods. We approached restoration from a conservative viewpoint. In seeding treatments, we used native grass species exclusively and did so only in narrowly defined target areas. Further, we defined the most vulnerable areas using vegetation and soil properties and their relationship to plant invasions after these three wildfires to develop a model predicting highly vulnerable areas to direct future restoration and to potentially reduce unnecessary post-fire treatments (Robichaud *et al*. 2000).

### *Patterns and mechanisms of vulnerability to weed invasion*

#### *Broad-scale patterns of vulnerability to weed invasion*

The relative vulnerability to weed invasion of each major type of habitat in MVNP can be predicted from basic vegetation and soils characteristics. At the scale of the entire park, mature or old-growth piñon–juniper woodlands growing on Mikim loam and Arabrab-Longburn soil series are most vulnerable to post-fire weed invasion. This is partially because mature piñon–juniper woodlands tend to have a relatively sparse ground cover of native herb and shrub species capable of rapid post-fire sprouting, and partially because Mikim loam and Arabrab soils have as-yet-undefined soil characteristics that apparently are very favorable for weed growth. (These two soil series also support the greatest abundance of weeds on unburned sites.) The second most vulnerable habitat is mature and old-growth piñon–juniper woodlands growing on other soil series. The sparse growth of native plants immediately after fire in piñon–juniper woodlands means that space and nutrients are readily available to support the establishment of non-native weed species (which generally require abundant light and nutrients). Once established, the most aggressive of these non-native species may persist for at least 13 years (and probably much longer) and compete with native forbs and grasses.

The least vulnerable type of vegetation to non-native invasions, at the scale of the entire park, is mountain shrubland. This can be attributed to the re-sprouting nature of dominant shrubs and forbs after fire – even where fire kills all above-ground vegetation and consumes most of the organic soil layer. The sprouting native species apparently take up available space and utilize available nutrients so quickly and efficiently that non-native species have limited opportunity to become established. Riparian vegetation, and other plant community types that contain a mix of sprouting and non-sprouting species, are intermediate in their vulnerability to non-native invasion. For all vegetation types, weeds are consistently more abundant in burned areas than in nearby unburned stands. Weeds also tend to be most abundant in years of normal or high precipitation, and are less abundant in extreme drought years like 2002 and 2003.

#### *Fine-scale patterns of vulnerability to weed invasion*

Broad-scale patterns of weed density were accompanied by very high standard errors, indicating that a great deal of additional variability exists at fine scales within each major vegetation type and between burned and unburned sites. At the scale of a $1000\,m^2$ plot, a greater number (richness) of native plant species was strongly correlated with a greater number of non-native species, indicating that habitats that support high native biodiversity are at the greatest risk of weed invasion. This trend is consistent with Stohlgren *et al*. (2003) and does not support the 'diversity–resistance' hypothesis of Elton (1958) and others (McCann 2000; Dukes 2001; Kennedy *et al*. 2002).

Weed density also was correlated with local soil properties at the scale of a $1000\,m^2$ plot, both within the perimeter of the 2000 Bircher and Pony fires and in nearby unburned areas. Two years after the fire, weed density was greater in sites with greater soil nitrate and a higher percentage of silt than in places where nitrate and percentage silt were lower. In unburned areas, weed density increased with increased soil nitrogen, phosphorus, and conductivity. These findings further support the idea that weeds thrive in the high soil nutrient conditions that typically characterize post-fire environments and that also tend to support higher native plant diversity in either burned or unburned areas. Findings from the present initial analysis of the effects of fire on soil characteristics and, in turn on non-native densities, suggest that the availability of nitrogen and phosphorus, as well as soil textural class, should be considered as important indicators of site invasibility.

The spatial model derived from soil and vegetation characteristics of Mesa Verde (Fig. 3) can be modified for other regions where post-fire weed invasions occur. Such a model informs and reduces potential mitigation, and may allow a reduction in area treated and prevent the need for broadcast seeding and other controversial means of treatment in use today (Robichaud *et al*. 2000; Keeley 2004).

### *Effectiveness of weed mitigation measures*

Following the 1996 Chapin 5 fire, a variety of weed mitigation techniques were applied to sites considered to be at the greatest risk of weed invasion. These methods included aerial seeding of native grass species in the fall of 1996, and chemical and mechanical eradication of localized thistle populations in 1997, 1998, and 1999. In 2003, average weed (primarily *Carduus nutans*) density was much greater in burned areas than in nearby unburned areas. However, *Carduus nutans* density was lower by two-thirds and native grass density was higher by 100-fold in the areas that received aerial seeding treatments than in areas that received no treatment. These results indicate that aerial seeding of native grasses *did* reduce the density of post-fire weeds and *did* increase the native component of the post-fire plant community. However, aerial seeding *did not* completely prevent weed invasion; 7 years after the fire, the non-native species were still present throughout the area that burned in 1996, although their densities were significantly lower where the aerial seeding treatment had been applied.

Herbicide treatment of the rhizomatous *Cirsium arvense* resulted in almost complete mortality. Mechanical treatment of *Carduus nutans* was effective only in areas where native grasses were present. Both species have persisted in burned areas that were not treated by any means. However, two of the less aggressive weed species, *Salola australis* and *Lactuca serriola*, both of which were abundant in the Chapin 5 burn 1 and 2 years post fire, had almost disappeared by 2003 from treated and untreated areas alike.

Overall, our analysis of the various weed mitigation measures suggests four general conclusions that may be applicable to future weed mitigation efforts. First, aerial seeding of native grasses is very effective at reducing weed densities and rapidly increasing the native grass component of the post-fire plant community, but seeding does not entirely prevent weeds from becoming established in burned areas. Second, chemical treatment is very effective at eradicating *Cirsium arvense*; however, because it is labor-intensive, it probably is feasible only in localized areas. Third, mechanical removal is effective at eradication of *Carduus nutans*, but only where native grasses are present. Like chemical treatment, mechanical eradication is labor-intensive and probably is not feasible over large areas. Finally, some of the less aggressive weed species may largely disappear within less than a decade even without treatment.

### Bromus tectorum *– a significant and increasing threat to ecological integrity in MVNP*

Our weed studies prior to 2003 focused on the most abundant and aggressive non-native species that we found in burned areas – notably *Carduus nutans* and *Cirsium arvense*. Prior to 2003, *Bromus tectorum* was not a major component of post-fire weed communities, nor was it common anywhere on the mesa tops in MVNP. Indeed, it was thought that the relatively high elevation, high summer precipitation, and cool temperatures that characterize MVNP would prevent *Bromus tectorum* from becoming important within the park. However, in 2003 dense stands appeared in many places throughout MVNP where it had not been conspicuous previously. New *Bromus tectorum* locations included areas at surprisingly high elevations, e.g. at ~2480 m elevation. Equally alarming was our finding of no significant difference in *Bromus tectorum* density in 2003 between areas that had been aerially seeded after the 1996 Chapin 5 fire and nearby areas that had received no treatment.

We regard this rapid proliferation and spread of *Bromus tectorum* in MVNP as a very serious threat to the long-term ecological integrity of park ecosystems. *Bromus tectorum* invasion elsewhere in the West has led to profound changes in native plant species diversity, community structure, and fire regime. A winter annual, this grass grows rapidly during late winter and early spring, potentially consuming much of the soil moisture needed by later-growing native plants. When dense stands of *Bromus tectorum* die and cure in early summer, they provide a continuous bed of highly flammable fuel, which can readily carry a relatively low-intensity but fast-moving fire. If *Bromus tectorum* continues to spread into recently burned areas in MVNP, it may cause a switch from the previous fire regime of infrequent fires, which occurred only during extremely dry periods, to a new fire regime of frequent fires. Because the native flora is adapted to the historical fire regime, a change of this kind could produce rapid and irreversible degradation of MVNP's native vegetation.

## Conclusion

Our data suggest that a conservative restoration approach following a high severity fire – seeding with native grasses obtained from the local region – reduces invasives, promotes native forb and grass community development, and can be feasible in large areas deemed vulnerable to invasion. A weed risk model, assembled from the distribution of 'functional groups' in the vegetation, soil series, and soil characteristics (percentage silt, levels of soil nitrate, net nitrogen mineralization, and available phosphorus) may assist managers in identifying the habitats most vulnerable to post-fire invasions. When modified for the local soil and vegetation characteristics, such a model may be successful in identifying invasible habitats within the burn and allow managers to more narrowly focus restoration activities, reducing the problems associated with broad-scale broadcast seeding and other non-specific mitigation treatments. Additional treatments using limited herbicide application or mechanical treatments, although locally effective, may not be feasible in extensive post-fire landscapes.

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